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A RECONSIDERATION OF THE MILLIPED GENUS *SIGMORIA,* WITH A REVISION OF *DELTOTARIA* AND AN ANALYSIS OF THE GENERA IN THE TRIBE APHELORIINI (POLYDESMIDA: XYSTODESMIDAE)

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INTRODUCTION

This paper reviews the genera in the xystodesmid milliped tribe Apheloriini (Xystodesminae) and provides diagnostic statements for those deemed valid. For *Sigmoria,* which is considered valid since the concepts of the older genus-group names, *Apheloria and Brachoria,* have not been critically analyzed, we present an expanded diagnosis, descriptions of 10 new species, redescriptions of five species, supplemental accounts of 15 species transferred into the genus, and additional information on distribution, ecology, and relationships. *Sigmoria* now consists of 65 species, with three divided into a total of nine subspecies. For *Deltotaria* we present a diagnosis, accounts of the gonopods of the two species in "sigmoid" terminology[3], diagnoses of the two subspecies of the type species, and distributional and ecological information. The paper concludes with analyses of the Apheloriini and the four principal xystodesmid tribes in eastern North America.

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We use five taxonomic categories throughout this work in reference to the Apheloriini: genera, subgenera, species groups, species, and subspecies. In various respects their usages are not traditional to xystodesmid classifications, and explanations are in order.

Genera are taxa with apparent geographic and lineage independence. Among the Apheloriini, *Sigmoria* is a cohesive geographic entity and forms a "mosaic" of largely allopatric or parapatric parts (subgenera, species groups, species, and subspecies). The other genera form their own mosaic patterns, which overlie each other and *Sigmoria* to varying degrees. Acceptance of this minimal generic concept allows us to remain within traditional limits of xystodesmid classification, because no clear autapomorphies have yet been found among gonopodal or somatic characters for many genera including *Sigmoria,* and there may be none. Consequently, it is geographic cohesiveness that gives these genera their apparent individuality or reality, which in turn justifies generic distinction. *Deltotaria,* however, is defined by an autapomorphy, the coxal apophysis. Thus, *Deltotaria* and *Sigmoria* are distinct, sympatric geographic entities, but only the former is defined cladistically.

Subgenera are not customarily employed in milliped classifications, and we do not advocate their use. However, our analysis of *Sigmoria* resulted in the recognition of eight major components, all of which have published genus-group names available. It is convenient to recognize these major entities, and we conserve the senior name at the subgeneric level. The subgenera may have one or more species groups, tend to be allopatric or parapatric, do not show clear patterns of lineage independence, and are difficult to relate in standard cladistic fashion. Lack of lineage independence is reflected by similarities (symplesiomorphies) between proximal elements of adjacent subgenera, which we think reflect ancestral continuities. This pattern is a prime reason why the major components are not separate genera; they are sections of a single geographic entity. We are convinced that seven subgenera are monophyletic; *Sigiria,* however, may be paraphyletic. Beginning with the first subgeneric account, that of *Rudiloria,* subgeneric assignment is indicated throughout the text either before or after the specific name, as for example "*ainsliei (Falloria).*" When two or more species in sequence belong to the same subgenus, the designation follows the last — thus "*pela, brooksi,* and *coronata (Dixioria).*"

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[3] The term "sigmoid" has no taxonomic value and refers collectively to the various apheloriine taxa whose gonopodal acropodites curve in a vaguely sigmoidal fashion. To standardize taxonomic treatments and to facilitate comparisons between species, Shelley (1981a) developed new terminology for these acropodites and divided them into sections or zones. This method of characterizing apheloriine acropodites has been used in subsequent papers and for simplicity is referred to as "sigmoid" terminology.

Species groups combine closely related species, some of which might unite as superspecies or even prove to be conspecific. They are geographically coherent and represent our estimates of specific relationships. In most cases these groups differ considerably from those proposed by Shelley (1981a).

Species are taxa which we hypothesize to be reproductive isolates, apparently segregated from geographically proximal taxa and not connected by intergrades. Evidence for separation comes in various forms. Ranges may be so proximal that discontinuities are abrupt, as between *pela* (Chamberlin) and *wrighti* Hoffman, and *translineata* Shelley and *lyrea* Shelley. Phenotypically different taxa such as *brooksi* Hoffman and *coronata* (Hoffman) that appear to be syntopic in part of their ranges also are considered reproductively isolated. Additionally, there may be a clear range disjunction between taxa that otherwise could be considered subspecies, the chief example being that of *rubromarginata* (Bollman) and *austrimontis* Shelley. Despite their residual intergrades, we consider both full species because genetic interchange is no longer possible; hence, the latter is elevated to specific status. The gap between *leucostriata* Shelley and *xerophylla* Shelley is occupied by several other taxa, and we consider this further evidence for reproductive isolation.

Subspecies are taxa which are reasonably homogeneous throughout their ranges but which connect with other such taxa through intergrade or intermediate forms. We reserve this category for *latior* (Brolemann), *trimaculata* (Wood), and *nigrimontis* (Chamberlin), geographically varied but clinally continuous species with uninterrupted ranges where gene flow is still possible.

The systematic treatment of *Sigmoria* in Part I proceeds in the clockwise geographic sequence of north to south to west, both among the subgenera and their component species groups. Species accounts vary. A few new records are presented for those previously discussed (Shelley 1981a), but otherwise they are merely listed. The new species are described; *houstoni* Chamberlin and *mimetica* (Chamberlin) are redescribed; and the treatments of the transferred species vary according to the depths of previous accounts, some being redescribed, some having gonopodal descriptions in "sigmoid" terminology, and others merely summarized. A new name is proposed for *Sigmoria simplex* Shelley, 1981a, to avert homonymy with *Croatania* *simplex* Shelley, 1977. Full synonymies are provided for the newly incorporated species; synonyms of previously included taxa are found in Shelley (1981a). To facilitate identifications we provide anatomical keys to subgenera and species of *Sigmoria* and a tabular presentation (Table 3) of geographical distributions for species of *Sigmoria* and *Deltotaria*. The keys refer to illustrations in this paper plus Shelley (1980a, 1981a and b, 1982, 1983a, 1984a); the table includes a color pattern code.

Holotypes of all pertinent nominal species were seen except those of *Polydesmus trimaculatus* (Wood), which is lost; *Fontaria lutzi* Jacot, for which clear illustrations and reasonably proximal material are available; and *Hubroria picapa* Keeton, *Fontaria pela* Chamberlin, and *Dixioria dactylifera* Hoffman, for which paratypes are available. Two requests to the NMNH failed to produce the holotype of *H. picapa,* which Keeton claimed to have deposited there both in his 1960 paper and in a 1976 letter to the senior author. He kindly loaned paratypes from his collection, and after his death in 1980, these were deposited in the FMNH and the personal collection of R.L. Hoffman. Type specimen notations are always of the senior synonym. Unless otherwise stated in the locality listings, collections were made by the senior author and assistants. The acronym GSMNP denotes the Great Smoky Mountains National Park; acronyms of sources of preserved study material cited in the text are as follows:

AMNH — American Museum of Natural History, New York, NY.
ANSP — Academy of Natural Sciences, Philadelphia, PA
AU — Department of Zoology and Entomology, Auburn University, Auburn, AL
FMNH — Field Museum of Natural History, Chicago, IL
FSCA — Florida State Collection of Arthropods, Gainesville, FL
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA
NMNH — National Museum of Natural History, Smithsonian Institution, Washington, DC
NCSM — North Carolina State Museum of Natural History, Raleigh, NC. The invertebrate catalog numbers of material from this collection are indicated in parentheses.
PMNH — Peabody Museum of Natural History, Yale University, New Haven, CT
RLH — Private collection of Richard L. Hoffman, Radford, VA
ROM — Royal Ontario Museum, Toronto, Ontario, Canada
RVC — Private collection of the late Ralph V. Chamberlin, now being accessioned by the NMNH.

UMN — Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, MN
WAS — Private collection of William A. Shear, Hampden-Sydney, VA

LITERATURE REVIEW

The papers pertaining to the species of *Sigmoria* in previous works (Shelley 1981a, 1983a) were discussed at those times; here major references on the additional taxa are summarized. The history of *Deltotaria* was reviewed by Hoffman (1961), the only additional citation being his (1979) inclusion of it in the tribe Apheloriini, where he said it consisted of five species in the southern Appalachian region.

The oldest species discussed herein, *trimaculata* Wood (1864, 1865), is one of four originally placed in *Fontaria* Gray (1832)[4]. One other, *F. rileyi* Bollman (1888), was proposed in the 19th century, and Chamberlin (1918a,b) added *F. mimetica* and *F. pela*.

In 1921 Chamberlin erected *Apheloria* for the new species *ainsliei* and *F. montana* Bollman, which was designated type species. Both were included under *Apheloria* by Chamberlin and Hoffman (1958), but Hoffman (1978a) observed that the genus was heterogeneous in its original proposal. Consequently, he removed *ainsliei* from *Apheloria* but left it unassigned. We agree with Hoffman's assessment and herewith place the species in *Sigmoria*.

In 1938 Jacot described *F. lutzi* from Keene, New Hampshire. A year later the number of pertinent nominal taxa increased dramatically, when Chamberlin (1939) proposed *A. keuka,* here placed in synonymy under the nominate subspecies of *trimaculata,* and the genera *Sigmoria, Sigiria,* and *Cleptoria,* with seven, one, and two species, respectively. Shelley (1981a) dealt with *Sigiria* and the species originally assigned to it and *Sigmoria,* and we can now report that *C. macra* Chamberlin is also properly assigned to the latter because its characters grade into those possessed by more "typical" forms. *Cleptoria* therefore becomes a subgenus of *Sigmoria.* Its second original species was *rileyi,* which Chamberlin (1939) transferred from *Fontaria.*

The decade of the 1940's brought more nominal species and the initial effort at reduction through synonymies. Chamberlin (1943) described *Sigmoria houstoni* from, supposedly, Houston, Texas, but it actually occurs in the Cumberland Plateau of southern Tennessee. Loomis (1943) suggested that *C. macra* was a synonym of *rileyi* and expressed doubt about the validity of *Cleptoria,* a most perceptive insight that we now agree with. Loomis' insight into relationships showed again in 1944, when he described *C. shelfordi.* He realized 40 years ago that this form was congeneric with *macra,* something that neither Hoffman (1967) nor Shelley (1980a, 1981b) perceived. Chamberlin (1947) proposed *Dixioria* for the new species, *dentifer,* which Hoffman (1956a) correctly synonymized with *pela,* in turn transferred from *Fontaria.* In 1949 Chamberlin described *Apheloria tortua;* and Hoffman added *A. antrostomicola, kleinpeteri,* and *picta,* four Virginia locality records for *trimaculata,* which Attems (1938) had transferred into *Apheloria,* and *Deltotaria coronata.*

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[4] Because of the extreme confusion surrounding this name, we agree with Hoffman (1979) that *Fontaria* should be placed on the list of officially rejected names in zoology.

The decade of the 1950's featured the Checklist, three papers by Hoffman, and one by Causey. Hoffman, (1950) summarized *Sigmoria,* which included the transfer of *mimetica* from *Fontaria,* and remarked that the absence of gonopodal drawings hampered determination of its generic position. However, he did not provide any, and *mimetica* still has not been illustrated. Hoffman (1951) identified four races of *Apheloria trimaculata* based on the shape and size of the middorsal spot. *Fontaria lutzi* was synonymized with the nominate subspecies, and *A. antrostomicola* and *A. tortua* were reduced to subspecific status. The fourth subspecies, *A. t. incarnata,* occurring in Ontario, Canada, was newly diagnosed. Causey's sole contribution to *Sigmoria* came in 1955, when she established the genus *Rudiloria* for the new species *mohicana.* Hoffman (1956a) transferred *Deltotaria coronata* into *Dixioria* and recognized two species: *dactylifera,* and *pela,* the latter with six subspecies. Chamberlin and Hoffman's checklist of the North American fauna (1958) listed without change the species from all previous studies except the last.

Keeton (1960) began the ensuing decade with the erection of *Hubroria* for the new species, *picapa.* The only other pertinent study of this period was the revision of *Cleptoria* by Hoffman (1967). He recognized five species — *marca; rileyi,* with two subspecies; *abbotti* and *bipraesidens,* both newly *diagnosed; and divergens* (Chamberlin) — and transferred *shelfordi* out of the genus but left it unassigned.

Recent contributions to the taxa under study include the diagnosis of *Apheloria guyandotta,* the transferral of *mohicana* into that genus, and the suppression of *Rudiloria* by Shear (1972). Hoffman (1979) assigned *Apheloria, Sigmoria, Cleptoria, Dixioria,* and *Hubroria,* to the new tribe Apheloriini along with *Croatania,* which Shelley (1977) established for four species in the Carolinas. *Rudiloria* was considered a synonym of *Apheloria* by Hoffman (1979), the most recent action on that taxon, although Hoffman (1978a) had revived it for 10 nominal species of *Apheloria.* The order of appearance of these two studies was reversed by publication delays. More recently Shelley (1980a) erected *Brevigonus* for *shelfordi* and (1981b) added a second species, *arcuatus*. Shelley (1981a) published a monograph on *Sigmoria* transferring *houstoni* and *mimetica* out of the genus but leaving them unassigned. In the final relevant work, Shelley (1983a) returned *divergens* to *Sigmoria*.

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Tourism (Santee State Park); Tennessee Department of Conservation (Cedars of Lebanon, Edgar Evins, Fall Creek Falls, Henry Horton, and Lake Radnor State Parks); the Parks and Historic Sites Division, Georgia Department of Natural Resources (Augusta Canal, Crooked River, Hard Labor Creek, Kolomoki Mounds, and Mistletoe State Parks); the State Parks Division, Alabama Department of Conservation and Natural Resources (Chattahoochee and Chewacla State Parks); and the Division of Recreation and Parks, Florida Department of Natural Resources (Torreya State Park). Cathy Wood typed and retyped the manuscript, and Renaldo G. Kuhler, NCSM scientific illustrator, prepared Figures 5, 14, 19, 25, 28, 32, 38, 42, 46, 61, 64, 70, 74, 78, 85, 89, 93, 98, 100, 106, 110, 116, 122, 128, 138, and 142. Henrik Enghoff (Zoologisk Museum, Copenhagen) and Peter Mundel (NMNH) provided valuable criticism throughout the manuscript; Mary Mikevich and Michael Schauff (Systematic Entomology Laboratory) added comments on the chapters on relationships. Lastly, the senior author wishes to express his deep gratitude to certain colleagues at the NCSM, who have both supported and encouraged his basic taxonomic research on millipeds throughout his employment. Financial support for this research was rendered in part by the National Science Foundation Grants Nos. DEB 7702596 and 8200556, and was used to fund necessary travel and subsistence, employment of field assistants, and publication costs.

PART I. REVISION OF SIGMORIA

by Rowland M. Shelley

Taxonomic Characters

The taxonomically important characters of *Sigmoria* are as listed previously (1981a), but with the inclusion of more species, they require elaboration. Most of these characters are found on the male gonopods, and in much of the eastern United States collection of males is mandatory for positive generic determinations. One exception is the northeast (New England, New York, Canada, and northern Pennsylvania and New Jersey), where *trimaculata* and *Apheloria corrugata* (Wood) are the only two apheloriine species. They can be distinguished by color pattern, the former having yellow middorsal spots and the latter displaying yellow metatergal stripes.

Coloration.— Color and color pattern are useful clues to the identity of an individual of either sex, and I (1981a) presented a table that now must be enlarged (Table 1). As before, all forms display a black metatergal base color and colored paranota, but a middorsal spot pattern is added to the

TABLE 1. Colors and color patterns of species and subspecies of *Sigmoria*

Pattern	Color	Taxa
Paranotal spots only	red, orange, or yellow	*stenoloba, latior latior,* some *latior* intergrades*, *simplex**
	red only	*australis*, macra, shelfordi, arcuata, robusta, abbotti, rileyi, saluda*
	yellow only	*catawba, simplex*, pela, dactylifera, brooksi, acuminata, coronata, watauga, wrighti*
Paranotal and mid-dorsal spots	both yellow, interior of latter sometimes tinted with red	*guyandotta, trimaculata*
Paranotal spots and metatergal stripes	both yellow to orange	*inornata*, areolata, latior munda**, some latior intergrades*, *simplex**
	both lemon yellow	*whiteheadi*
	both orange	*planca*
	both red	*inornata*, truncata, sigirioides, quadrata, laticurvosa, stibarophalla, latior munda*, latior hoffmani,* some latior intergrades*, *rubromarginata, triangulata, nigrimontis, australis*, divergens, austrimontis, persica, serrata, bipraesidens, haerens, divaricata, thrinax*
	both violet or purple	*stenogon, disjuncta*
	both white or light yellow	*leucostriata*
	paranota red, stripes blue	*fumimontis, bidens, translineata, lyrea, tuberosa, xerophylla, ainsliei, aphelorioides, prolata, mimetica, crassicurvosa, pendulata, picapa, forficata, houstoni, abbreviata*
	paranota red, stripes white	*nantahalae*

*taxa that are polymorphic for color

several stripe and paranotal spot patterns of before. The last category is also expanded, since some species display only red or yellow paranota in addition to the highly variable colors of *latior latior* and *stenoloba.* In addition to the color variation sometimes seen along the inner margin of the paranotal spots and metatergal stripes, the size of the middorsal spots in *guyandotta* and *trimaculata* varies from small discrete dots, as found in northern populations of the latter, to large semilunar blotches that may even spread laterad into diffuse, indistinct stripes connecting with the paranota markings. To avoid confusion, these species are listed only in the "paranotal and middorsal spots" category, but this variation should be noted because it demonstrates how spot and stripe patterns relate to each other. Table 1 summarizes the most common colors and color patterns for each species and subspecies of *Sigmoria,* omitting occasional variations exhibited by such taxa as *bidens, translineata, divergens, ainsliei, mimetica,* and *pendulata.* Taxa that are commonly polymorphic for color and/or pattern are indicated by an asterisk. A clear paranotal spot and metatergal stripe pattern is evident on preserved material of *mohicana* and *rigida,* but since the colors are unknown, they are omitted. I have not personally collected them, and there is no indication of living colors in either the literature or on labels with the specimens.

The various colors and patterns tend to cluster throughout the range of *Sigmoria* and also within that of the Apheloriini (Figs. 148-150, 159). These phenomena are discussed in Part V.

Sterna.— Except for the more densely pilose condition in *tuberosa, the* only aspects of the sterna that aid in determinations are the configuration and degree of development of the process of the 4th sternum and, to a lesser extent, those of the 5th. Variation of the processes is as described previously (Shelley 1981a), and Table 2 presents updated information on that of the 4th sternum. The newly included species add to each of the three columns to bring the totals to 37 species in which the process is shorter than the widths of the adjacent sterna, 19 in which they are subequal, and 9 in which the projection is longer.

Gonopodal Characters.— Most of the specific characters in *Sigmoria* obtain in aspects of the male gonopods. The newly included species increase the scope of variation and require supplemental accounts for each zone of the acropodite plus ones on thickness, the *in situ* arrangements, and the prefemoral process.

1. *In situ arrangements.—* The *in situ* arrangements of the newly included species fit, for the most part, the overlapping, crossing, and parallel patterns described previously, although a telopodite will occasionally be dislodged giving an atypical arrangement. The only new configurations oc-

TABLE 2. Length of process of 4th sternum in males in species of *Sigmoria*

Shorter (than widths of adjacent coxae)	Subequal	Longer
latior	*quadrata*	*tuberosa*
stenoloba	*laticurvosa*	*catawba*
areolata	*translineata*	*saluda*
stibarophalla	*lyrea*	*yemassee*
inornata	*fumimontis*	*forficata*
truncata	*ainsliei*	*abbotti*
sigirioides	*aphelorioides*	*arcuata*
stenogon	*bidens*	*robusta*
nantahalae	*macra*	*bipraesidens*
leucostriata	*rileyi*	
xerophylla	*shelfordi*	
rubromarginata	*pela*	
austrimontis	*brooksi*	
triangulata	*acuminata*	
whiteheadi	*coronata*	
nigrimontis	*wrighti*	
disjuncta	*watauga*	
prolata	*haerens*	
mimetica	*trimaculata*	
crassicurvosa		
pendulata		
picapa		
abbreviata		
houstoni		
australis		
simplex		
divergens		
dactylifera		
mohicana		
rigida		
guyandotta		
planca		
persica		
agrestis		
serrata		
divaricata		
thrinax		

cur in *ainsliei, aphelorioides,* and the subgenera *Rudiloria* and *Dixioria.* In *ainsliei* the acropodites intertwine (Fig. 89), which is really a manifestation of the overlapping pattern caused by the circular configuration. Conversely, in most males of *aphelorioides* the acropodites lie above and below each other (Fig. 85) and rarely overlap. In the subgenus *Rudiloria* the telopodites are oriented differently on the coxa and face mediad. Here and in *Dixioria* they are directed transversely across the body and tend to insert in the opposite side of the aperture instead of extending over the anterior margin and lying between the 7th legs. This arrangement is shown in Figures 5 and 14, in Shear (1972, Fig. 1) for *guyandotta,* and in Hoffman (1978, Fig. 2) for *t. trimaculata.*

2. *Prefemoral process.*— With more species and more diversity, the prefemoral process loses all effectiveness as a specific criterion. A basally divided process occurs in four species rather than two (*ainsliei, forficata, translineata,* and *lyrea*), and the configuration in *bidens* is approached in proximal populations of *prolata.* Thus, even in these cases, determinations based solely on the process are inadvisable. Moreover, species are now known without a process or with only a vestige — *pendulata, bipraesidens, rileyi, guyandotta* and *mohicana.*

3. *Characters of the acropodite. a) Thickness.*— The newly added species included those with the heaviest, most massive gonopods in the genus (*rileyi, abbotti, bipraesidens, robusta, crassicurvosa,* and *pendulata*). In a few, such as *mohicana, trimaculata, pela,* and *wrighti,* the acropodites are rather thin and fragile, and similar to those of *stenogon* and *sigirioides.* The others fall between these extremes.

b) General curvature. — It is in general curvature that the newly added species depart the most from those previously included in *Sigmoria,* and the generic concept must now be broadened to encompass forms whose acropodites circumscribe a complete or nearly complete loop. Three species are involved: *ainsliei, aphelorioides,* and *trimaculata.* In these the anterior bend and apical curve are more or less continuous through the peak, so that the acropodal regions are obscure. The overall configuration is of a smoothly continuous circle, with the tip overlapping or nearly overlapping the basal zone in medial view. Futhermore, many of the newly added species do not possess coplanar basal and distal zones. The latter region angles generally laterad from the peak, and is coplanar with the peak in *houstoni* and *picapa.* Heretofore, only *stibarophalla, disjuncta,* and *divergens* had laterally directed distal zones, but this character is also displayed by *australis, prolata, mohicana,* the subgenus *Dixioria,* and certain species of the *translineata* group of the subgenus *Falloria.*

c) Basal zone. — The basal zone has more taxonomic significance than formerly thought. Previously, the tubercles of *tuberosa* were the only modifications of the outer surface of this region, but with the inclusion of the southeastern lowland forms, more specializations are known. The medial edge of the basal zone is deeply emarginate and notched in *catawba* and *saluda* and sinuous to shallowly notched in *simplex* and *yemassee,* and the basalmost projection is enlarged in the first three. *Sigmoria arcuata, rileyi, abbotti, robusta,* and *shelfordi* have a single basal projection that ranges from a large spur to a strong, distinct spine, which may be homologous with the basalmost projection in *catawba, saluda,* and *simplex.* In the *trimaculata* group the basal zone is directed mediad rather than anteriomediad.

d) Anterior bend. — The anterior bend varies from well defined, in species like *brooksi, rigida,* and *australis,* to broad and poorly defined in those with circular acropodites.

e) Peak. — The peak is tilted laterad in the *mimetica* group of *Falloria,* exposing the undersurface in medial view. It is also much thicker in those species with heavy, massive acropodites.

f) Apical curve and distal zone. — As stated earlier, more species are now known with laterally directed distal zones that are not coplanar with basal zones. In *houstoni* and *picapa* the distal zone is actually coplanar with the peak. Extremely short distal zones, coplanar with the basal zones and directed perpendicularly from the peak, are found in five species of the subgenus *Cleptoria.* The opposite extreme is found in *ainsliei* and *trimaculata,* where the region completes the loop of the acropodite and overlaps the basal zone. *Sigmoria shelfordi* joins *truncata* in lacking this section, the acropodite terminating at the distal extremity of the peak. Additional lobes and flanges are found on the distal zones of *pendulata* and *crassicurvosa.*

g) Tip. — Except for variants of such species as *aphelorioides* and *arcuata,* which have reflexed tips, all the newly added taxa have simple, blunt to acute, terminations.

h) Medial flange. — Considerable additional variation is known for the medial flange. It can be located much more proximally and arise well onto the basal zone. In the forms of *Cleptoria* with heavy acropodites it loses some of the laminate character, becoming correspondingly thick and heavy. The ultimate condition obtains in *bipraesidens,* where the flange is not a lamina but a thickening or swelling of the entire medial surface of the peak with the general contours of the flange in *rileyi* when viewed ventrally. In the *mimetica* group the flange is narrow and the peak is tilted laterad, so that in medial view the undersurface is visible and the flange is obscure.

Likewise, the lamella is obscured in medial view in the subgenus *Rudiloria,* because the basal zone which carries it is directed mediad. *Sigmoria ainsliei, aphelorioides,* and *nantahalae* and the subgenus *Dixioria* lack the flange.

i) Tooth. — Additional species with a tooth on the medial margin of the acropodite include *rigida* and the seven species of the subgenus *Dixioria.* Others, like *rileyi, robusta, catawba,* and *saluda* have broadly rounded or triangular distal lobes on the flange, which may represent the tooth. A small, sharp accessory tooth arising from the under surface of the acropodite at or near the location of the marginal tooth is also present in all species of *Dixioria* except *dactylifera.* The tooth or teeth are usually located on the peak but may also be on the distal zone.

j) Lateral flange. — The lateral flange is absent from most newly added species, and in most of the others it is not laminate. In the southeastern species with heavy acropodites (*rileyi, robusta, abbotti, catawba* and *saluda*) it is more lobe-like, more ventrad than laterad, and poorly demarcated from the acropodite stem in the first three, where it forms the highest point of the acropodite arch.

k) Prostatic groove. — The prostatic groove crosses from the medial to the lateral sides of the acropodite at various positions depending on how the telopodite is situated on the coxa and whether or not the peak is tilted.

l) Solenomerite. — In most species of *Sigmoria* the prostatic groove runs along the main stem of the acropodite, avoiding flanges, lobes, and other adornments, and opens terminally at the tip of the distal zone. In the subgenus *Cheiropus,* however, the acropodite is either apically divided or there is a small subterminal structure on which the groove opens. This structure, or the terminal division carrying the groove, is called the solenomerite, and its position and configuration are taxonomically important.

Genus SIGMORIA Chamberlin

Previous gonopodal descriptions and that of the 6th sternum (Shelley 1981a, 1983a) are rewritten to accommodate the newly incorporated species. Other somatic features are unchanged.

Diagnosis. — Coxa without apophysis; acropodite curving in variable sigmoid to coiled or circular configurations, with or without variable flanges, lobes, or teeth on different zones, but always without a transverse groove or cingulum on outer surface.

Description. — Sternum of segment 6 with or without variable convex recession or excavation between 7th legs to accommodate apical curvatures of acropodites.

Gonopods *in situ* with variable configurations; usually with each acropodite extending mediad beyond midline of aperture and over- or under-lapping other acropodite proximal to midlength in midline, curving slightly anteriolaterad over opposite side of aperture then back over midline with tips curving dorsad and crossing, apical curvatures extending to varying lengths over anterior margin of aperture and sternum of segment 6; some species with acropodites crossing only once in peak or apical curve regions in midline of aperture, apical curves extending anteriad only slightly beyond anterior margin of aperture; others with acropodites not overlapping but medial edges touching or nearly touching in midline and extending anteriad in subparallel arrangement over anterior margin of aperture and sternum of segment 6, apical portions of curvatures in these forms projecting either dorsad or dorsolaterad; still others with acropodites curving dorsad over opposite side of aperture and either touching or approaching opposite coxa and lying in front of and behind each other or curving laterad toward midline and overlapping opposite member. Coxa moderate to large, without apophysis, connected by membrane only, no sternal remnant. Telopodite set terminally on coxa, latter not projecting distad beyond prefemoral region. Prefemur moderate in size, with or without variable prefemoral process, latter ranging from nubbinlike vestige to long, massive structure extending well beyond tip of acropodite, linear to bisinuate, simple or divided basally into two long, nearly equal components, or divided apically and bifurcate. Acropodite thin and fragile to thick and massive, with torsion, curved through one or more vertical planes in vaguely sigmoidal to loosely coiled or circular configurations as seen *in situ* and in medial and lateral views, configurations as follows: basal zone extending subventrad from prefemur; bent sharply or broadly anteriad (anterior bend) from 1/4 to 1/2 of total acropodal length; usually curved sharply or broadly dorsad or laterad apically (apical curve) near 2/3-3/4 length forming arc with variable diameter; portion between anterior bend and apical curve (peak of arch) coplanar with basal and distal zones or bowed mediad and not coplanar with latter regions, flattened or high and gently rounded in medial view, extending to or beyond level of prefemoral process; region forming apical curve (distal zone) varying in length, either projecting nearly directly dorsad, curved inward into acropodite arch and essentially coplanar with basal zone, or bent abruptly laterad, curving through more than one vertical plane, and not coplanar with basal zone, occasionally coplanar or nearly coplanar with peak, either of subequal width throughout most of length (except apically) or tapering smoothly and continuously to acuminate tip. Basal zone variable in length, inner surface usually directed anteriad, occasionally mediad, with or without variably laminate flange on medial surface and adornments on outer surface, latter including densely packed tubercles, a row of dentate spurs, or single basal spines; medial edge usually entire, occasionally variably expanded and finely scalloped or deeply and irregularly notched; lateral edge occasionally expanded and lamellate. Peak of arch variable in length and width, usually with inner surface directed toward arch, occasionally tilted laterad and facing mediad, with or without flange of variable length, width, and configuration on medial edge, arising from proximal part of basal zone to proximal part of peak, usually terminating from near midlength of peak to proximal part of distal zone, with or without variable laminate to spiniform tooth arising from medial edge or outer surface distal to flange, separated to varying lengths from flange, occasionally fused to latter; occasionally with small, sharp accessory tooth on undersurface at level of marginal tooth. Distal zone present or absent; when present with or without variable flanges or lobes proximally on both medial and lateral sides, one or both often arising on distal extremity of peak and distally on medial side; also with or without long, narrow, laminate flange on lateral side, arising near beginning of apical curve, terminating proximal to tip, flange occasionally modified into subtriangular lobe, long narrow subrectangular projection, or greatly enlarged and swollen, forming outermost point on acropodite arch; usually without but occasionally with teeth; when absent sometimes replaced by variably positioned solenomerite, best viewed laterally. Termination variable; either blunt or acuminate unmodified end of peak or distal zone; or small, reflexed lamina on medial edge directed at sharp angle (often perpendicularly) from distal zone; termination occasionally angled from distal zone but not separated into distinct lamina. Prostatic groove arising in pit on prefemur, running along stem of acropodite and crossing from medial to lateral sides at various locations, opening terminally on tip of distal zone or on reflexed lamina when present.

Females agreeing essentially with males in somatic features, except paranota usually more strongly depressed, creating appearance of more highly arched or vaulted body.

Distribution. — As currently understood (Fig. 145), *Sigmoria* occupies a large, contiguous, irregular area and five smaller, disjunct ones. The former extends from Ontario and northern New England to northeastern Florida, and longitudinally from the outer coastal Plain of the Carolinas and Georgia, the Blue Ridge Province of Virginia, and the New England Province, to piedmont Georgia, the Ridge and Valley Province of Tennessee, and Central Ohio. One disjunct area encompasses most of the Cumberland Plateau,[5] eastern Highland Rim, and Nashville Basin of Tennessee.[6] Another is located mostly in the Coastal Plain of south-central Alabama, ranging northward slightly into the Fall Zone. The third spans the Chattahoochee and upper Appalachicola Rivers in the Coastal Plains of southwestern Georgia, southeastern Alabama, and the adjacent part of Florida; and the fourth is located in extreme southern Georgia and the northern part of peninsular Florida. The fifth disjunct area, in the Cumberland Plateau of north-central Alabama and shown by the dot, is represented by a single male of *rileyi,* which became available as the paper was being drafted. The lacunae in Tennessee and those between the more southern disjunct areas are slightly over 40 miles wide and may be sampling artifacts that will eventually be joined. However, I have not found representatives there in nearly 10 years of field work and show them to accurately depict present knowledge. The blank area in south-central Georgia is around 90 miles in diameter and though nearly surrounded by *Sigmoria,* seems likely to survive additional field work. *Sigmoria* thus inhabits seven physiographic provinces and 17 states plus Ontario. The total north-south length is over 1,000 miles, and that from the Atlantic Ocean to central Tennessee is around 550 miles. The Alabama River seems a likely western distributional limit in Alabama.

Species. — Sixty-five, with three consisting of nine geographic races.

KEY TO SUBGENERA OF SIGMORIA

1. Color of metatergal stripes contrasting with that of paranota or both either white or pale yellow .... *Falloria* Hoffman
   Metaterga either uniformly black, variably spotted middorsally, or with stripes concolorous with paranota but not white or pale yellow 2

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[5] The local name, Cumberland Plateau, is used in this paper to refer to the southern part of the Appalachian Plateaus Physiographic Province.

[6] The Nashville Basin and the surrounding Highland Rim are the southernmost sections of the Interior Low Plateaus Physiographic Province.

2. Gonopods *in situ* with acropodites extending mostly mediad and projecting over opposite side of aperture, occasionally with sides tilted and leaning over anterior margin 3
   Gonopods *in situ* with acropodites extending mostly anteriad, projecting well beyond anterior margin of aperture and inserting between legs of segment 6 4
3. Caudolateral corners of paranota rounded through midbody segments; acropodite usually with accessory tooth arising from undersurface at or distal to level of tooth; metaterga uniformly black, never with spots or stripes .... *Dixioria* Chamberlin
   Caudolateral corners of paranota rounded only on anteriormost segments; acropodite without accessory tooth; color variable, metaterga usually with spots and stripes ... . *Rudiloria* Causey
4. Acropodites either with distal zones curving strongly laterad and obscured in medial view by stems or medial flanges, or with variably positioned solenomerites replacing distal zones .... *Cheiropus* Loomis
   Acropodites without solenomerites; distal zones visible in medial views 5
5. Acropodites usually massive and heavily sclerotized; basal zones usually with variable spines or teeth on outer or medial surface 6
   Acropodites thin and fragile to moderate, never massive; basal zones without modifications 7
6. Basal zones with variable teeth or variably notched expansions on proximomedial edges; prefemoral processes large to enormous, usually extending beyond tips of acropodites .... *Croatania* Shelley
   Basal zones with at most a single spine on outer surfaces; prefemoral processes small to absent .... *Cleptoria* Chamberlin
7. Acropodites either with reflexed tips or with this general configuration .... *Sigmoria* Chamberlin
   Tips of acropodites simple, blunt to acuminate .... *Sigiria* Chamberlin

KEY TO SPECIES OF SIGMORIA
(based primarily on adult males)

The difficulty of devising a key to the variable species of *Sigmoria* is greatly magnified by the addition of more congeners than were in the original revision (Shelley 1981a). Even less can now be said about a given species that does not also apply to another, and it is harder to compose couplets so as not to exclude important variants. Qualifying modifiers such as "usually" are therefore found throughout the key, because of the high frequency of exceptional variants. Also necessary are relative comparisons and subjective criteria like thickness, whose utility depends upon one's experience with "sigmoid" xystodesmids. For these reasons and to facilitate usage, most couplets contain more than one comparative criterion. In the following key the three subdivided species are treated as species, so all subspecies and intergrades key out at the same couplet. Except for lateral flanges, most characters of dissected gonopods are best seen in medial view, particularly those involving comparisons such as "...extending beyond level of distal zone." The few other instances when the lateral perspective is desirable are so stated. Figure numbers and generalized range descriptions are given to enhance the key. To avoid repetition and to distinguish them from drawings in this paper, illustrations in my previous revision (Shelley 1981a) are indicated by an asterisk after the number. References are cited for figures in other papers.

As all species of *Sigmoria* display vivid pigmentation, and the colors and patterns vary considerably, a checklist (Table 3) is presented after the key in which the distribution by state and color pattern is tabulated. Thus, where locality and color are known, determinations may be easier with this table than with the anatomical key. The two complement each other nicely, and the forms of *Deltotaria* are also included in the table for the sake of completion.

1. Gonopods with variably positioned solenomerites, best visible in lateral perspective 59
   Without this character 2
2. Gonopods with variable medial flanges, occasionally vestigial 12
   Without this character 3
3. Acropodite configuration circular, distal zone curving broadly into arch in medial view, extending beyond prefemoral process and overlapping or nearly overlapping basal zone; tooth absent 4
   Acropodite configuration otherwise, either resembling number 7, an inverted L, or curving broadly and continuously to but not beyond level of prefemoral process; tooth present 5
4. Prefemoral process divided basally into two long, unequal components; distal zone coplanar with basal zone (Figs. 90-91); Knox, Sevier, and Blount cos, TN .... *ainsliei* (Chamberlin)
   Prefemoral process simple, upright, and acuminate; distal zone curving sublaterad from peak, not coplanar with other sections; (Figs. 86-87); Swain Co. NC, to McMinn Co., TN .... *aphelorioides*, new species
5. Acropodite with minute, sharply pointed accessory tooth arising from under surface of acropodite stem or main tooth at or distal to latter 6
   Without this character 11
6. Outer margin of distal extremity of peak greatly expanded into broadly rounded lobe; accessory tooth arising from base of main tooth; prostatic groove crossing to lateral surface at anterior bend; latter sharp, well defined (Figs. 39-40); Washington Co., VA, and Johnson Co., TN .... *brooksi* (Hoffman)
   Outer margin of distal extremity of peak at most only faintly expanded, not lobe-like; accessory tooth arising from acropodite stem; anterior bend broad, poorly defined; prostatic groove crossing to lateral side on prefemur (Figs. 20-22, 26, 29-30, 33-36) 7
7. Acropodite configuration a flattened, open arch, overhanging and extending slightly beyond level of prefemoral process; peak linear; distal zone short, terminating well above level of prefemoral process (Figs. 26, 29-30) 8

Acropodite configuration a smooth, continuous curve, arch overhanging and extending slightly beyond level of prefemoral process; peak gently curved and rounded, apex at midlength; distal zone relatively long, extending to or near level of prefemoral process (Figs. 20-22, 33-36) 9

8. Tooth present (Figs. 29-30); Tazewell Co., VA, to Watauga Co., NC .... *coronata* (Hoffman)

Tooth absent (Figs. 26-27); Johnson Co., TN .... *acuminata* (Hoffman)

9. Accessory tooth arising distal to tooth, fully visible in medial view (Figs. 35-36); Watauga and Wilkes cos., NC .... *watauga,* new species

Accessory tooth arising at same level as tooth (when present), partly obscured in medial view (Figs. 20-22, 33-34) 10

10. Tooth always present, quadriform, apically dentate (Figs. 33-34); Johnson Co., TN, to Caldwell Co., NC .... *wrighti* (Hoffman)

Tooth present or absent, triangular to spiniform (Figs. 20-24); Carter Co., TN, to McDowell Co., NC .... *pela* (Chamberlin)

11. Tooth large, extending in medial view well below level of distal zone and nearly to that of prefemoral process, inner apical corner produced, extending into arch; lateral flange absent (Figs. 43-44); corners of paranota rounded beyond midlength; paranota yellow, metaterga black, without stripes; Ashe Co., NC .... *dactylifera* (Hoffman)

Tooth subequal in length to that of distal zone, but short, barely projecting below peak, terminating well above level of prefemoral process; lateral flange present (Figs. 63-64*); corners of paranota rounded only in anterior half of body; paranota red, metatergal stripes white; Swain Co., NC, to Towns and Union cos., GA .... *nantahalae* Hoffman

12. Prefemoral process usually present; occasionally vestigial 18

Prefemoral process usually absent 13

13. Acropodite of normal or moderate thickness or thin and fragile, latter poorly sclerotized 14

Acropodite thick and massive, heavily sclerotized 16

14. Basal zone with basal spine on outer surface (Shelley 1981b, Figs. 3-5); Pickens to Abbeville cos., SC .... *arcuata* (Shelley)

Without this character 15

15. Distal zone flared, lamellate (Fig. 9); Wyoming Co., WV to Menifee Co., KY .... *guyandotta* (Shear)

Distal zone of nearly equal width throughout except for tip, without lamellae (Fig. 11); Ashland Co., OH .... *mohicana* (Causey)

16. Peak flat and relatively long, about 1/3 of acropodite length; distal zone relatively short, terminating well above level of prefemur, directed perpendicularly from peak, forming rectangular acropodal arch (Figs. 50-51, 57-58) 17

Peak short, high, and rounded; distal zone relatively long, terminating at level of prefemoral process, arch an inverted U (Fig. 123); Putnam and Dekalb cos., TN .... *pendulata,* new species

17. Distal zone relatively broad, sides curving and converging to blunt tip; medial flange thick but distinctly laminate (Figs. 50-51); Clarke Co., GA, to Lee and Jefferson cos., AL .... *rileyi* (Bollman)

Distal zone relatively narrow, inner edge straight, outer curving inward to acuminate tip; medial flange represented by thickening of entire medial surface of peak (Figs. 57-58); Jackson Co., GA .... *bipraesidens* (Hoffman)

18. Distal zone and apical curve absent; acropodite terminating at distal extremity of peak 19

Distal zone and apical curve present, length and configuration variable 20

19. Medial flange arising on basal zone and terminating on distal extremity of peak; acropodite relatively thick and heavy, with or without proximal spine on outer edge of basal zone, with or without short, acute spur on medial or outer surfaces of peak (Shelley 1980a, Figs. 7-12); Oconee to McCormick cos., SC .... *shelfordi* (Loomis)

Medial flange arising on proximal part of peak and terminating just proximal to tip; acropodite relatively thin and blade-like, without spines or spurs (Figs. 37-38*); Yancey and Mitchell cos., NC .... *truncata* Shelley

20. Basal zone with teeth, spines, and/or tubercles on medial or outer surfaces (Figs. 47-48, 53-54, 62-63, 92-93*; Shelley 1977, Figs. 1, 3-4, 6) 21

Without these features, surfaces of basal zone smooth 27

21. Proximomedial edge of basal zone expanded and irregular, with small denticulations to sharply acute teeth and spines 22

Medial edge of basal zone smooth and entire, not expanded 25

22. Prefemoral process terminating below level of distal zone (Figs. 47-48); Chester to Berkeley cos., SC .... *simplex* (Shelley)

Prefemoral process large, extending to or beyond level of distal zone (Shelley, 1977, Figs. 1, 3, 6) 23

23. Prefemoral process apically bifurcate (Shelley 1977, Fig. 3); Laurens to Aiken cos., SC .... *saluda* (Shelley)

Prefemoral process simple, not bifurcate 24

24. Prefemoral process of approximately uniform width except near tip, bisinuately curved; proximomedial expansion of basal zone small and inconspicuous, with only small denticulations (Shelley 1977, Fig. 6); Beaufort and Jasper cos., SC .... *yemassee* (Shelley)

Prefemoral process subglobose basally, distal 1/3 narrower and bent into arch; proximomedial expansion broad, irregularly notched (Shelley 1977, Fig. 1); Lincoln Co., NC, to Chester Co., SC .... *catawba* (Shelley)

25. Outer margin of basal zone with dense cluster of minute tubercles (Figs. 92-93*); Swain Co., NC .... *tuberosa* (Shelley)

Outer margin of basal zone with basal, acute spine 26

26. Distal zone with outer margin continuous with lateral flange (lobe), without indentation, sides broadly rounded and converging to blunt tip; medial flange conspicuous, terminating in rounded lobe (Figs. 62-63); Oconee and Anderson cos., SC .... *robusta,* new species

Distal zone sharply demarcated from lateral flange (lobe) by deep indentation, sides gently curved and converging to acuminate tip; medial flange inconspicuous, without distal lobe (Figs. 53-54); Hart to Burke cos., GA .... *abbotti* (Hoffman)

27. Acropodite with peak tilted laterad, exposing under-surface in medial view; course of prostatic groove visible in medial view up to distal extremity of peak or proximal part of distal zone (Figs. 111, 117, 120) 28

Orientation of peak normal or tilted mediad 29

28. Acropodite massive, heavily sclerotized; distal zone with broadly rounded lobe at midlength on medial surface or with terminal medial lamina; tip a short, acuminate, and laminate projection from apex of distal zone (Figs. 117-120); Smith and Dekalb cos., TN .... *crassicurvosa,* new species

Acropodite moderately thick and heavy; distal zone without modifications; inner corner produced to form tip (Figs. 111-112); Robertson to Maury cos., TN .... *mimetica* (Chamberlin)

29. Prefemoral process divided from base to midlength into two long, prominent, nearly equal components (Figs. 94-96, 99-100, 68-69*, 72-73*)..................... 30

Prefemoral process with or without subterminal spurs or at most only shallowly or apically bifurcate, components small and usually unequal........................ 33

30. Distal zone long, curving broadly well below level of uppermost component and nearly to level of prefemoral division; tip pseudoreflexed (Figs. 72-73*); Swain Co., NC, and Blount Co., TN .... *lyrea* Shelley

Distal zone short, terminating above prefemoral components; tip blunt or acuminate 31

31. Acropodite with rounded lobe on lateral edge at apical curve, peak tilted mediad exposing lateral margin in medial view; distal zone coplanar with basal zone; tip blunt (Figs. 68-69*); Swain Co., NC, and Blount Co., TN .... *translineata* Shelley

Acropodite without lobe on lateral margin; orientation of peak normal; distal zone curving generally laterad from peak, not coplanar with basal zone; tip acuminate... 32

32. Prefemoral process divided near midlength, components relatively short, straight, and nearly equal; medial flange short and narrow, arising near midlength of peak, margin gently rounded; distal zone short, barely projecting into arch (Figs. 99-100); Bledsoe and Van Buren cos., TN........................ *abbreviata,* new species

Prefemoral process divided basally, components moderate to long, lateral one broadly or sharply curved ventrad near midlength; medial flange variable, arising from proximal part of basal zone to peak, broadly rounded or triangular on distal extremity of latter; distal zone moderately long, curving well into arch (Figs. 94-96); Scott to Hamilton cos., TN.................................... *forficata,* new species

33. Basal zone with inner surface directed mediad; medial flange narrow located entirely on basal zone, inconspicuous in medial view (Figs. 2, 6, 15).................... 34

Basal zone with inner surface directed generally anteriad; medial flange with configuration and position variable, not located entirely on basal zone, conspicuous or inconspicuous.. 35

34. Acropodite with distinct spiniform or triangular tooth near midlength of peak (Figs. 15-16); metaterga with stripes along caudal margins; Kanawha, Clay, and Nicholas cos., WV.. *rigida,* new species

Without this character; metaterga usually with variable middorsal spots, occasionally with stripes; Ontario and northern New England to Washington Co., VA .... *trimaculata* (Wood)

35. Prefemoral process long, extending beyond level of distal zone (Figs. 79-83)........ 36

Prefemoral process terminating well below level of distal zone 37

36. Distal zone curving dorsad (downward in medial view) from peak, coplanar with basal zone; tooth present on proximal part of distal zone, widely separated from medial flange; prefemoral process greatly enlarged to globose basally (Figs. 80-81*); Sevier Co., TN... *bidens* (Causey)

Distal zone directed laterad from peak, not coplanar with basal zone; tooth absent; prefemoral process variable but at most only moderately swollen basally (Figs. 79-83); Sevier Co., TN................................... *prolata,* new species

37. Distal zone curving generally laterad from peak, not coplanar with basal zone...... 38

Distal zone with variable length, directed generally dorsad from peak, essentially coplanar with basal zone 44

38. Medial flange arising on basal zone or proximal part of peak, variably broad, obscuring at least narrow part of acropodite stem in medial view (Figs. 71, 75, 25*, 27*; Shelley 1983, Fig. 2) 39

Medial flange located entirely on distal zone, peak and basal zone entirely visible in medial view (Fig. 129*); Oconee Co., SC, to Dawson Co., GA.. *disjuncta* Shelley

39. Medial flange long and narrow, arising on basal zone, terminating in broadly rounded lobe at midlength of distal zone; ventral surface of prefemoral process convex distad (Figs. 103-104); Franklin, Grundy, and Marion cos., TN ..... *houstoni* Chamberlin

Medial flange terminating proximal to distal zone, configuration variable; prefemoral process without excavations.. 40

40. Prefemoral process relatively long and bisinuately curved, extending beyond midlength of basal zone and terminating near level of distal zone (Figs. 107-108); Morgan Co., TN .... *picapa* (Keeton)

Prefemoral process relatively short, not bisinuate, much shorter than half the length of basal zone, terminating well below level of distal zone.. 41

41. Medial flange thick and heavily sclerotized, not especially laminate; prostatic grove crossing from medial to lateral sides on basal zone (Shelley 1983a, Figs. 2-3); Spartanburg and Pickens cos., SC, to Polk and Transylvania cos., NC.. *divergens* Chamberlin

Medial flange variably broad but thin and laminate, weakly sclerotized; prostatic groove crossing to lateral side at anterior bend.. 42

42. Acropodites thick and massive, heavily sclerotized, too large to overlap in aperture, one thus directed mediad and other projecting anteriad over most of 6th sternum; prefemoral process directed anteriad and parallel to peak, not toward distal part of acropodite (Figs. 25-28*); Buncombe, McDowell, and Rutherford cos., NC .... *stibarophalla* Shelley

Acropodite moderately thick and heavy, overlapping normally over aperture and extending beyond anterior margin; prefemoral process directed toward distal part of acropodite 43

43. Medial flange moderately broad, distally triangular; distal zone short, in lateral view not extending beyond level of broad, triangular part of medial flange (Figs. 71-72); Hampton Co., SC, to Wilcox Co., AL.. *australis,* new species

Medial flange narrow, only slightly wider distad, not triangular; distal zone moderately long, in lateral view curving into arch and well beyond level of medial flange (Figs. 75-76); Patrick Co., VA.. *whiteheadi,* new species

44. Medial flange arising on basal zone, terminating on peak; peak with or without spur on outer surface near anterior bend; lateral flange not laminate, in form of broadly rounded lobe projecting ventrad and forming highest point of arch, poorly demarcated from distal zone (Figs. 65-67); Greenville to Newberry cos., SC .... *macra* (Chamberlin)

Medial flange absent from basal zone, arising on peak or distal zone; peak without spurs; lateral flange present or absent, laminate when present, not forming highest point of arch 45

45. Medial flange on proximal portion of peak (Figs.3*, 31*, 45*, 57*, 76*, 84*, 88*) 46

Medial flange on distal zone (Figs. 97*, 102*, 105*, 108*, 114*) 56

46. Medial flange small, not obscuring stem of acropodite in medial view; distal zone with opposing proximal lobes on medial and lateral margins, lateral lobe larger (Figs. 84*, 88*) 47

Medial flange larger, obscuring at least small section of stem of acropodite in medial view; distal zone either without lobes or with lobe only on lateral side 48

47. Portion of distal zone distal to lobes relatively long, bent sharply into arch; lateral flange present (Figs. 84-85*); paranota and metatergal stripes white to light yellow; Cocke and Sevier cos., TN .... *leucostriata* Shelley

Portion of distal zone distal to lobes relatively short, only slightly curved into arch; lateral flange absent (Figs. 88-89*); paranota red, metatergal stripes blue; McMinn Co., TN, to Gilmer Co., GA .... *xerophylla* Shelley

48. Lateral flange absent 49

Lateral flange present 51

49. Arch of acropodite subtending a square; peak flattened, length nearly equal to distal zone (Figs. 45*, 47*); Lexington, Saluda, and Edgefield cos., SC .... *quadrata* Shelley

Arch of acropodite otherwise; peak gently curved or rising to apex at beginning of apical curve, shorter or longer than distal zone 50

50. Peak of arch gently curved, shorter than distal zone; medial flange relatively short, margin acuminate; distal zone relatively long, projecting dorsad from peak (Fig. 41*); Yancey Co., NC .... *sigirioides* Shelley

Peak of arch with apex distad at beginning of apical curve, much longer than distal zone; medial flange relatively long and narrow, margin variable; distal zone relatively short, projecting dorsad from peak or curved into arch (Figs. 31*, 33*); Mitchell, Yancey and McDowell cos., NC .... *inornata*, new name

51. Medial flange short, obscuring at most only short section of stem of acropodite; peak of arch rounded, anterior bend and apical curve more or less continuous through peak, poorly defined; distal zone curved but not projecting significantly into arch (Figs. 51*, 53*); Aiken Co., SC .... *laticurvosa* Shelley

Medial flange longer, obscuring long section of acropodite stem; peak not rounded, anterior bend and apical curve sharp and well defined, not continuous through peak; distal zone curved or straight, projecting well into arch 52

52. Apical curve bisinuate, with two inward bends into arch; lateral flange variable, absent, triangular, or rectangular (Figs. 57*, 59-60*); Transylvania and Henderson cos., NC .... *stenogon* Chamberlin

Apical curve smoothly rounded and continuous, forming arc with variable diameter; lateral flange present, usually long and narrow, occasionally with margin projecting and irregular, never triangular or rectangular 53

53. Acropodite thick and heavy; peak tilted mediad, exposing lateral margin in medial view; tooth absent (Fig. 76*); Blount Co., TN .... *fumimontis* Shelley

Acropodite moderately thick and heavy; peak oriented normally, lateral edge obscured in medial view; tooth present 54

54. Peak flexed ventrad at midlength; tooth attached to lamina of medial flange but well separated from lobe of latter; tip simple (Fig. 21*); Buncombe Co., NC .... *areolata* Shelley

Peak relatively flat; tooth present or absent, not attached to lamina of medial flange; tip reflexed 55

55. Medial flange narrow, poorly demarcated from stem of acropodite, depth much less than that of apical curvature; when present, tooth usually well separated from

medial flange, often greatly reduced and rounded (Figs. 12-15*); Wilkes and Catawba cos., NC . . . . *stenoloba* Shelley

Medial flange broad to large, well demarcated from stem of acropodite; depth equal to or greater than that of apical curvature; when present, tooth located at distal extremity of medial flange, usually subacuminate (Figs. 3*, 8*, 9*); southern West Virginia to southern South Carolina . . . . *latior* (Brolemann)

56. Distal zone tapering to acuminate tip; medial and lateral flanges large and conspicuous; peak of arch gently rounded (Figs. 97*, 105*) 57

Distal zone of nearly equal width throughout except for tip; latter blunt; flanges reduced, medial often vestigial; peak either curved or flattened (Figs. 108-112*, 114-121*, 123-124*, 126-127*); Greene and Unicoi cos., TN, to Buncombe and McDowell cos., NC . . . . *nigrimontis* (Chamberlin)

57. Lateral flange triangular, located entirely on peak; distal zone bisinuately curved distad, directed toward prefemoral process (Fig. 105*); Cocke Co., TN, and Madison Co., NC . . . . *triangulata* Shelley

Lateral flange with margin broadly rounded, occurring from distal extremity of peak to midlength of distal zone; latter bent sharply inward into arch at termination point of flanges (Figs. 97*, 100*, 102*) 58

58. Acropodites in medial view showing profile of arch and distal zone; edge of medial flange visible in medial view, face directed anteriad; prefemoral process relatively long, recurved at midlength and directed toward distal zone, simple or bifurcate with one component usually much longer (Fig. 97*); Sevier and Cocke cos., TN, to Transylvania Co., NC . . . . *rubromarginata* (Bollman)

Distal zone twisted mediad revealing part of face of medial flange or all of faces of medial and lateral flanges in medial view; proximal portion of arch visible, distal obscured by flanges; bend of distal zone partly or completely obscured by flanges in medial view; prefemoral process variably short and straight, usually bifurcate with subequal components (Figs. 100-103*); Buncombe to Burke cos., NC. . . . . *austrimontis* Shelley

59. Acropodite with row of distinct spurs on basal zone (Shelley 1982, Figs. 4, 8, 12) 60

Without this character 62

60. Acropodite apically trifurcate, solenomerite directed away from gonopod along axis of acropodite; latter a broad, continuous curve, anterior bend poorly defined (Shelley 1982, Figs. 11-12); Polk and Henderson cos., NC. . . . . *thrinax* (Shelley)

Acropodite apically blunt to subacute, with at most two terminal projections; solenomerite located beneath distal extremity of peak, directed perpendicularly and laterad to peak; acropodite bent sharply at 1/3 to 1/2 length, anterior bend well defined 61

61. Solenomerite fused to undersurface of peak; spurs moderate in size, located entirely on basal zone (Shelley 1982, Figs. 3-4); McDowell, Buncombe, and Henderson cos., NC . . . . *haerens* (Shelley)

Solenomerite a separate bisinuate process, narrowly segregated from peak; spurs moderate to large in size, extending around anterior bend to base of lateral flange on peak (Shelley 1982, Figs. 7-8); Rutherford, Henderson, and Polk cos., NC . . . . *divaricata* (Shelley)

62. Acropodite broadened distad into cupulate expansion or cap; solenomerite either beneath and partly or completely obscured by cap, or located laterad at its base. 63

Acropodite relatively narrow; widest basally, tapering smoothly to acuminate tip; solenomerite about half the length of acropodite, arising near base of, and running subparallel to, acropodite (Shelley 1984a, Figs. 10-11); Fall Zone of central Georgia .... *persica* (Hoffman)

63. Solenomerite distinctly visible on lateral side of acropodite at base of expansion; except for eastern populations, margin of expansion not strongly serrated (Shelley 1984a, Figs. 3-7); Thomas Co., GA, to Hernando Co., FL .... *planca* (Loomis)

Solenomerite located beneath cap and partly or completely obscured; margin of expansion strongly serrated 64

64. Acropodite in form of continuous, broadly curved arc, extending in medial view beyond level of prefemur; margin of expansion with a single row of up to 12 teeth; solenomerite a thickened, sclerotized boss (Shelley 1984a, Figs. 13-15); Charleston Co., SC, to Clarke and Burke cos., GA .... *agrestis* (Loomis)

Acropodite in form of inverted L, stem relatively straight, bent sharply anteriad at level of cap, overhanging prefemur in medial view; margin of expansion highly serrate, with two or more rows of variable teeth; solenomerite a thin, falcate projection tucked under teeth, distal to boss (Shelley 1984, Figs. 19-22); Liberty Co., GA, to Duval Co., FL .... *serrata* (Shelley)

SIGMORIA (RUDILORIA) Causey, new status

Rudiloria Causey, 1955:28. Chamberlin and Hoffman, 1958:47. Jeekel, 1971:285. Hoffman 1978:6

Type species. — *Rudiloria mohicana* Causey, 1955, by original designation.

Diagnosis. — Metatergal color pattern variable, with spots or stripes of varying widths and diameters, at least partly concolorous with paranotal markings; gonopods *in situ* with acropodites extending mostly over opposite side of aperture, not projecting anteriad between legs of segment 6; acropodites relatively thin and fragile, oriented on coxa with inner surface directed mediad, with narrow medial flange present on basal zone, largely undetectable in medial view because of acropodal orientation; tip simple.

Remarks. — Occurring from Virginia to Canada and northern New England, the subgenus *Rudiloria* occupies the largest and most northerly range in *Sigmoria s. lat.* At first glance most of the species do not appear congeneric with *latior (Sigmoria)* or the species formerly described (Shelley 1981a) as having acropodites shaped like the number 7, but the most extreme forms with circular acropodites connect with the latter through a continuum of intermediate forms and there are important similarities with known species of *Sigmoria s. lat.* in North Carolina and Tennessee. Over the years these intermediate forms have received names which I retain, there being no compelling reason to do otherwise. More collecting is needed in eastern Kentucky, northern West Virginia, southern and eastern Ohio, and western Pennsylvania before their true statuses can be determined. In the only case where ample material is available, *trimaculata* from the counties

TABLE 3. Distribution of species and subspecies of *Sigmoria* and *Deltotaria* by state and color pattern

Code for color pattern:

1. With yellow to red paranotal spots, metaterga entirely black.
2. With yellow to red paranotal spots, metaterga with middorsal spots.
3. With yellow or orange paranotal spots and metatergal stripes.
4. With red paranotal spots and metatergal stripes.
5. With violet or purple paranotal spots and metatergal stripes.
6. With white or pale yellow paranotal spots and metatergal stripes.
7. With red paranotal spots, metaterga with blue stripes.
8. With red paranotal spots, metaterga with white stripes.
9. With yellow or orange paranotal spots, metatergal stripes, and sparkling sheen.
10. Colors and pattern unknown.

Taxon	Code	AL	FL	GA	SC	NC	TN	KY	VA	WV	OH	MD	PA	NY	New England	Ontario
Sigmoria																
(Rudiloria)																
1. *t. trimaculata*	2,3								+	+		+	+	+	+	+
2. *t. kleinpeteri*	2								+							
3. *trimaculata* intgds.	2								+							
4. *guyandotta*	2							+		+						
5. *mohicana*	10										+					
6. *rigida*	10									+						
(Dixioria)																
7. *pela*	1					+	+									
8. *acuminata*	1						+									
9. *coronata*	1					+	+		+							
10. *watauga*	1					+										
11. *wrighti*	1					+	+									

12. *brooksi*	1						+		+	
13. *dactylifera*	1					+				
(Sigmoria)										
14. *l. latior*	1					+	+		+	+
15. *l. munda*	3,4				+	+				
16. *l. hoffmani*	4				+					
17. *latior* intgds.	1,3,4				+	+				
18. *stenoloba*	1					+				
19. *quadrata*	4				+					
20. *laticurvosa*	4				+					
(Croatania)										
21. *catawba*	1				+	+				
22. *saluda*	1				+					
23. *simplex*	1,3,4				+					
24. *yemassee*	10				+					
(Cleptoria)										
25. *rileyi*	1	+		+						
26. *abbotti*	1			+						
27. *bipraesidens*	4			+						
28. *robusta*	1				+					
29. *arcuata*	1				+					
30. *shelfordi*	1				+					
31. *macra*	1				+					
(Cheiropus)										
32. *australis*	1,4	+	+	+	+					
33. *stibarophalla*	4					+				
34. *divergens*	4,5				+	+				
35. *haerens*	4					+				
36. *divaricata*	4					+				
37. *thrinax*	4					+				

Taxon	Code	AL	FL	GA	SC	NC	TN	KY	VA	WV	OH	MD	PA	NY	New England	Ontario
38. *agrestis*	4			+	+											
39. *serrata*	4		+	+												
40. *planca*	3		+	+												
41. *persica*	4			+												
(Sigiria)																
42. *rubromarginata*	4					+	+									
43. *austrimontis*	4					+										
44. *whiteheadi*	3								+							
45. *triangulata*	4					+	+									
46. *n. nigrimontis*	4					+										
47. *n. intermedia*	4					+	+									
48. *n. angulosa*	4					+										
49. *n. unicoi*	4						+									
50. *sigirioides*	4					+										
51. *truncata*	4					+										
52. *inornata*	3,4					+										
53. *areolata*	3					+										
54. *stenogon*	5					+										
55. *disjuncta*	5			+	+											
(Falloria)																
56. *nantahalae*	8			+		+										
57. *leucostriata*	6						+									
58. *xerophylla*	7			+			+									
59. *apheloroides*	7					+	+									

60. *translineata*	7			+	+
61. *fumimontis*	7				+
62. *lyrea*	7			+	+
63. *ainsliei*	7				+
64. *bidens*	7				+
65. *prolata*	7				+
66. *tuberosa*	7			+	
67. *forficata*	7				+
68. *houstoni*	7				+
69. *abbreviata*	7				+
70. *picapa*	7				+
71. *mimetica*	7				+
73. *pendulata*	7				+
73. *crassicurvosa*	7				+
Deltotaria					
b. brimleii	4	+		+	+
b. philia	4,9	+	+	+	
brimleii intgds.	4				+
lea	9		+	+	

of western Virginia, it is possible to combine nominal species to form subspecies and synonyms.

The acropodites of the forms of *Rudiloria* are relatively thin and fragile and curve more mediad than anteriad, thus projecting more over the opposite side of the aperture than over the anterior margin and the 6th sternum. The inner surface of the basal zone is directed mediad, and since the thin, narrow medial flange is located chiefly in this region, it it barely detectable in medial view. The most variable aspect of the acropodites is the distal zone, which can be moderate to very long, overlapping the basal zone and forming a loop or circular acropodite. This condition is similar to that in *ainsliei, aphelorioides, (Falloria)* and species of *Apheloria*. The prefemoral processes range from absent to short and triangular to moderately long and uncinate. The subgenus is comprised of five known forms in a single species group, the *trimaculata* group. Two forms are considered races of a single species.

Components. — *trimaculata* (Wood) [*t. trimaculata, t. kleinpeteri* (Hoffman)], *mohicana* (Causey), *guyandotta* (Shear), *rigida* new species.

Sigmoria (Rudiloria) trimaculata (Wood), new combination

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on distal part of basal zone and with variable color pattern, paranota yellow, metaterga with yellow, red, or orange markings on caudal edges ranging from small, discrete middorsal spots to variable semilunar blotches diffusing into paranotal markings and becoming stripes; gonopods with following diagnostic characters: prefemoral process moderately long, uncinate; acropodite thin and fragile, forming completely or nearly complete, broadly symmetrical, loop overhanging and extending well beyond level of prefemoral process; basal zone with inner surface directed mediad; anterior bend and apical curve poorly defined; peak gently curved to flattened, continuous through anterior bend and apical curve with basal and distal zones; latter either coplanar with basal zone or curving through several planes and not coplanar with basal zone, extending downward from peak in medial view then curving into arch and terminating in acute, falcate tip, with or without broadly rounded lobes at midlength; medial flange inconspicuous in medial view.

Remarks. — This species has the largest range in the genus, extending from Canada north of Lake Ontario to southwestern Virginia. There is marked stability in the configuration of the gonopods from central Virginia northward, but in Giles County, the acropodite begins to widen at midlength of the distal zone (base of the upwards curve). South of Giles

County there is a broad lobe at this position whose proximal part is oriented perpendicularly to the medial field of view and whose distal part lies in this plane. Samples from Mountain Lake Biological Station and northern Giles County display intermediate conditions ranging from a slightly wider acropodite at this point to a small rounded lobe. I therefore recognize two subspecies of this assemblage, the oldest available name being *trimaculata* (Wood, 1864), assigned to a population of the northern form from Susquehannah County, Pennsylvania. The oldest available name from the range of the southern race is *kleinpeteri* (Hoffman 1949). Two names were proposed for intergrade forms, *tortua* (Chamberlin 1949) and *picta* (Hoffman 1949), and for the sake of convenience, I place them in synonymy under the nominate subspecies.

Sigmoria (Rudiloria) trimaculata trimaculata (Wood) Figs. 1-3

Polydesmus (Fontaria) trimaculata Wood, 1864:6; 1865:223-224, Figs. 53-54.
Fontaria lutzi Jacot, 1938:571-572, Fig. 1.
Apheloria trimaculata: Attems, 1938:170. Loomis, 1944:173 (in part). Hoffman, 1949:378.
Apheloria keuka Chamberlin, 1939:10-11, pl. 4, Fig. 32. Chamberlin and Hoffman, 1958:19 **NEW SYNONYMY.**
Apheloria coriacea (nec Koch): Chamberlin, 1947:25, Fig. 5.
Apheloria tortua Chamberlin, 1949:101, Fig. 23. **NEW SYNONYMY.**
Apheloria antrostomicola Hoffman, 1949:372-374, pl. 26, Figs. 1-2. **NEW SYNONYMY.**
Apheloria picta Hoffman, 1949:376-378, pl. 26, Figs. 5-6. **NEW SYNONYMY.**
Apheloria trimaculata trimaculata: Hoffman, 1951:2-3, Fig. 1b. Chamberlin and Hoffman, 1958:20.
Apheloria trimaculata antrostomicola: Hoffman, 1951:3-4, Fig. 1c. Chamberlin and Hoffman, 1958:20-21.
Apheloria trimaculata incarnata Hoffman, 1951:4-5, Fig. 1a. Chamberlin and Hoffman, 1958:21. **NEW SYNONYMY.**
Apheloria trimaculata tortua: Hoffman, 1951:5-6, Fig. 1d. Chamberlin and Hoffman, 1958: 21.
Rudiloria trimaculata: Hoffman, 1978, Figs. 2, 5.
Apheloria (Rudiloria) trimaculata trimaculata: Kevan, 1983:2968.

Type specimens. — Not known to exist; the type locality is in Susquehannah Co., PA (Wood 1864, 1865).

Diagnosis. — Peak relatively flat; distal zone at most only slightly wider at midlength (base of upwards curve), without lobes.

Color in Life. — Variable. Most forms with yellow paranota and concolorous, yellow mid-dorsal spots on caudal edges of otherwise black metaterga, the spots varying in size from small, discrete circles to semilunar blotches spreading laterally along segment margins; some forms with spots connecting by thin line with paranotal markings, others with broad yellow stripes along caudal edges showing little or no evidence of middorsal spots (see also Hoffman 1949, 1951).

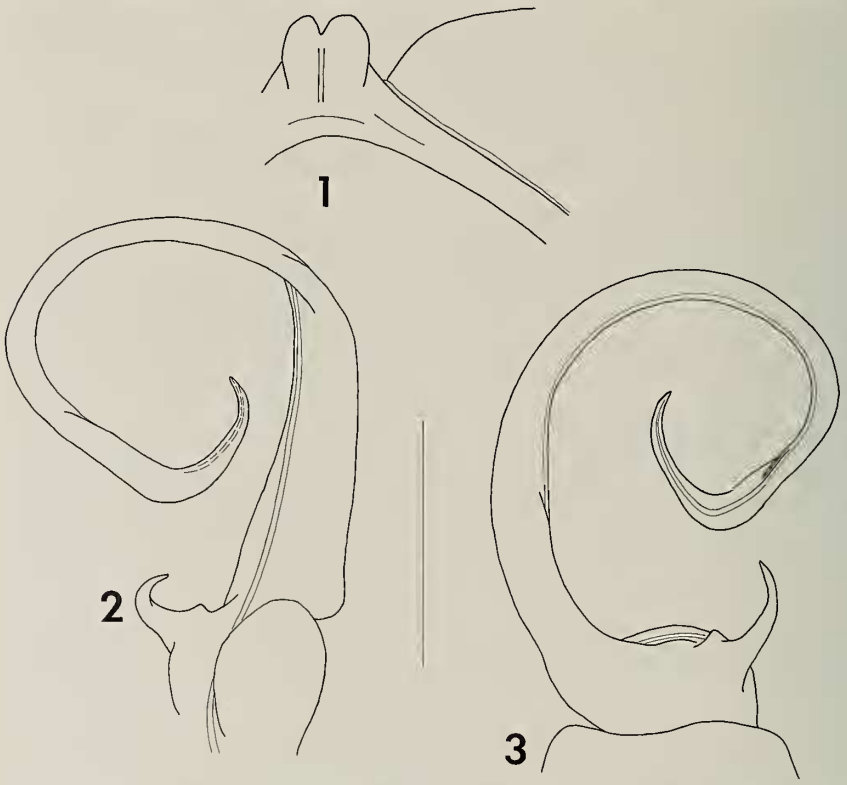
Male from Tucker Co., WV. — Length 33.9 mm, maximum width 7.7 mm, W/L ratio 22.7%, depth/width ratio 59.7%. Segmental widths as follows:

collums 6.4 mm	15th 7.4
2nd-3rd 7.1	16th 7.1
4th 7.4	17th 6.1
5th-14th 7.7	18th 4.9

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.4 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres 2>3>5=6>4>1>7. Genae without impressions. Facial setae as follows: epicranial 1-1, interantennal absent, frontal 1-1, genal 2-2, clypeal about 10-10, labral about 18-18, merging with clypeal series and continuing for short distance along genal border, about 4 setae per side.

Dorsum smooth, polished, moderately coriaceous on paranota. Collum broad, ends not produced beyond those of following tergite. Paranota moderately depressed, continuing slope of



Figs. 1-3. *Sigmoria (Rudiloria) trimaculata trimaculata.* 1, process of 4th sternum of male from Tucker Co., WV, caudal view. 2, telopodite of left gonopod of the same, medial view. 3, the same, lateral view. Scale line = 1.00 mm for all figures.

dorsum, caudolateral corners rounded through segment 10, becoming blunt and progressively more acute caudally. Peritremata thin but distinct, moderately elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum moderately long, apically divided, length equal to widths of adjacent coxae (Fig. 1); 5th sternum with two low, paramedian knobs between anterior legs and elevated flattened areas between posterior legs; 6th sternum flattened, with very slight convex impression on caudal surface. Postgonopodal sterna flat and plate-like, with bicruciform impressions on segments 8-9 and variably broad, shallow, central impressions on remaining segments. Coxae with low, blunt tubercles beginning on segment 9, becoming longer and sharper caudally; prefemoral spines arising on segment 5, becoming progressively more acute posteriorly.

Gonopodal aperture ovoid, 3.4 mm wide and 1.8 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Hoffman, 1978, Fig. 2) with acropodites curving mediad across midline of aperture, curving dorsad over opposite side then laterad toward midline, overlapping opposite member. Gonopod structure as follows (Figs. 2-3): Prefemoral process moderately long, acute, and falcate, directed mediad, with low, basal spur. Acropodite thin and fragile, in form of flattened loop nearly forming complete circle, overhanging and extending well beyond level of prefemoral process; basal zone relatively long, inner surface directed mediad, sides tapering distad, without modifications; anterior bend moderately broad; peak moderately long, flattened, not continuous with basal zone; apical curve broad, poorly defined; distal zone long, curving broadly downward from peak, linearly into arch, then upwards in a short, linear stretch terminating in acute, falcate tip, sides diverging slightly proximad and broadest at base of upwards curve, tapering smoothly and continuously thereafter; tip directed toward peak in medial view. Medial flange narrow and inconspicuous in medial view, arising on basal zone and blending with medial edge at anterior bend. Lateral flange absent. Prostatic groove crossing to lateral surface at anterior bend, continuing to terminal opening.

Female from Tucker Co. — Length 40.7 mm, maximum width 7.4 mm, W/L ratio 18.2%, depth/width ratio 78.4%. Cyphopods *in situ* with receptacles visible in aperture, valves directed dorsad. Receptacle large, hood-like, enveloping valves, surface rugulose. Valves small, equal, surfaces finely granulate.

Variation. — The gonopods of *trimaculata* are constant throughout the range and do not change with changes in color pattern.

Ecology. — The material I collected in West Virginia and New York was discovered under moist hardwood litter in sheltered sites in deciduous forests.

Distribution. — Northern New England and southern Ontario to west-central Virginia, mostly in upland provinces. This species and *Apheloria corrugata* (Wood), also found in Ontario, are the only two xystodesmids known from eastern Canada, although *Pleuroloma flavipes* Rafinesque may occur in southern Ontario (Shelley 1980b, Kevan 1983). The range of *trimaculata,* around 550 miles long, is the longest documented to date in the Apheloriini. It spans many large rivers, including the St. Lawrence, Connecticut, Hudson, Delaware, Susquehannah, and Potomac. Material was examined as follows:

CANADA. — ONTARIO: *Durham Co.,* Kendal, M, 30 May 1966, and M, 19 July 1967, I.M. Smith (ROM). *Leeds Co.,* Charreys Locks, M, 29, May 1973, J.C.E. Riotte (ROM). *Halton Co.,* Speyside, F, 10 May 1964 (ROM). *Frontenac Co.,* Gull Lake nr. Arden, M, 4 September 1948, R.E. Crabill (NMNH).

UNITED STATES. — MAINE: *Oxford Co.,* Norway, F, date unknown, O. Harger (PMNH).

NEW HAMPSHIRE. — *Sullivan Co.,* Corbin Park, M, date unknown, B.L. Brooks (MCZ). *Rutland Co.,* Tweed River, M, 10 September 1934, collector unknown (UMN). *Bennington Co.,* Beartown, M, 9 June 1954, F.P. Rindge (AMNH).

MASSACHUSETTS. — Berkshire Co., Mt. Greylock, M, 15 June 1936, C.H. Blake (MCZ); and Williamstown, M, 14 June 1936, R. Dow (MCZ).

NEW YORK. — *Steuben Co.,* Lake Keuka, M, September 1905, collector unknown (RVC). *Essex Co.,* Keene Valley, 2M, 22 June and 21 July 1917, H. Notman (AMNH). *Greene Co.,* near Lanesville on NY hwy. 214, 6M, 7F, 18 August 1978 (NCSM A2402). *Ulster Co.,* Phoenicia, M, 25 July 1909, L.J. Barnum (AMNH).

PENNSYLVANIA. — *Potter Co.,* locality unknown, M, F, 3 July 1906, H.W. Fowler (ANSP). *Schuykill Co.,* Tuscarora St. Pk., 5M, 3F, 2 August 1981, H.W. Levi (MCZ).

WEST VIRGINIA. — *Tucker Co.,* along WV hwy. 32, 5.5 mi. E. Lanesville, Monogahela Nat. For., 7M, F, 23 August 1978 (NCSM A2412).

VIRGINIA. — *Highland CO.,* 2 mi. N Williamsville, Bull Pasture R. Gorge, 3M, F, 4 June 1972, R.L. Hoffman (RLH). *Bath Co.,* locality unknown, M, 2F, date and collector unknown (MCZ). *Rockbridge Co.,* Vesovius, F, 11 August 1971, R.H. Perry (RLH). *Alleghany Co.,* 2 mi. NW Clifton Forge, M, 3F, 14 June 1947, R.L. Hoffman (RLH); W side Potts Mtn., 2F, 18 July 1982 R.L. Hoffman (RLH); 8 mi. SW Lowmoor, 16 June 1947, R.L. Hoffman (NMNH).

Remarks. — Because color and color pattern are variable in many eastern xystodesmids, I do not think subspecies should be based solely on these characters. They should be accompanied by corresponding changes in the gonopods as in *latior (Sigmoria).* This was my philosophy with *Pleuroloma* (Shelley 1980b) and races were not recognized in *P. flavipes* Rafinesque. As shown in Table 1, several species of *Sigmoria s. lat.* are polymorphic for color and most have at least an occasional variant, so differences in color or color pattern are not a good basis for taxonomic decisions. The patterns in *t. trimaculata* are also more diverse than previously thought, as a yellow transverse stripe variant occurs in West Virginia.

Additional literature records of *trimaculata* are as follows: Susquehannah Co., PA (Wood 1864, 1865); Keene, Cheshire Co., NH (Jacot 1938); Ithaca, Tompkins Co., NY (Chamberlin, 1939, Loomis 1944); Potter Co., PA, and Garrett Co., MD (Chamberlin 1947); near Staunton and Lyndhurst, Augusta Co., VA (Hoffman 1949); and an unspecified site in Quebec, Canada (Kevan, 1983).

Sigmoria (Rudiloria) trimaculata kleinpeteri (Hoffman), new combination, new status Figs. 4-7

Apheloria trimaculata (nec Wood): Loomis, 1944:173 (in part).

Apheloria kleinpeteri Hoffman, 1949:375-376, Pl. 26, Figs. 3-4. Chamberlin and Hoffman, 1958:19.

Type specimens. — Male holotype (NMNH) and two male paratypes (RLH) collected by R.L. Hoffman and H.I. Kleinpeter, 30 June 1947, from Burkes Garden, Tazewell Co., Va. Female allotype (NMNH) collected by J.E. Graf, 5 June 1940, at same locality.

Diagnosis. — Peak gently curved; distal zone with broadly rounded lobes at midlength (base of upwards curve), the proximal one perpendicular to field of vision in medial view, the lateral one visible from this respective.

Variation. — The gonopods of *kleinpeteri* are uniform and do not vary appreciably from the condition in the holotype.

Ecology. — Unknown.

Distribution. — Western Virginia and adjacent southern West Virginia. Material was examined as follows:

WEST VIRGINIA. — *Mercer Co.,* Bluefield, East River Mts., M, F, 25 June 1961, R.L. Hoffman (RLH); and along US hwy. 52 above Bluefield, 2M, 20 June 1968, R.L. Hoffman (RLH).

VIRGINIA. — *Giles Co.,* W of Thessalia, near head of Sugar Run, 2M, 3 August 1980, R.L. Hoffman (RLH). *Bland Co.,* 2 mi. S. Long Spur, W side of Little Walker Mtn., F, 16 October 1966, R.L. Hoffman (RLH). *Tazewell Co.,* Burkes Garden, F, 5 June 1940, J.E. Graf (NMNH), M, 30 June 1947, R.L. Hoffman and H.I. Kleinpeter (NMNH), and M, July 1970, collector unknown (RLH). TYPE LOCALITY. *Wythe Co.,* 3 mi. ESE Wytheville, E slope Sand Mtn., F, 1 June 1981, R.L. Hoffman (RLH). *Washington Co.,* along VA hwy. 80 at Hayters Gap, 2M, 8 June 1974, D.W. Ogle (RLH); bluffs on N. Fork Holston R., 4M, 2F, 11 May 1981, D.W. Ogle (RLH); and Brumley Gap, 4M, 24 May 1978, R.L. Hoffman (RLH).

Sigmoria (Rudiloria) trimaculata intergrades

The samples of *trimaculata* from Mountain Lake Biological Station, in northern Giles County, Virginia, display conditions intermediate between those of the two subspecies. They vary from a slightly wider distal zone at midlength to a small rounded lobe at this point, the latter being illustrated by Hoffman (1949, Figs. 5-6). The names *Apheloria tortua* and *A. picta* have been assigned to these forms, and are synonymized with the nominate race. Specimens were examined as follows:

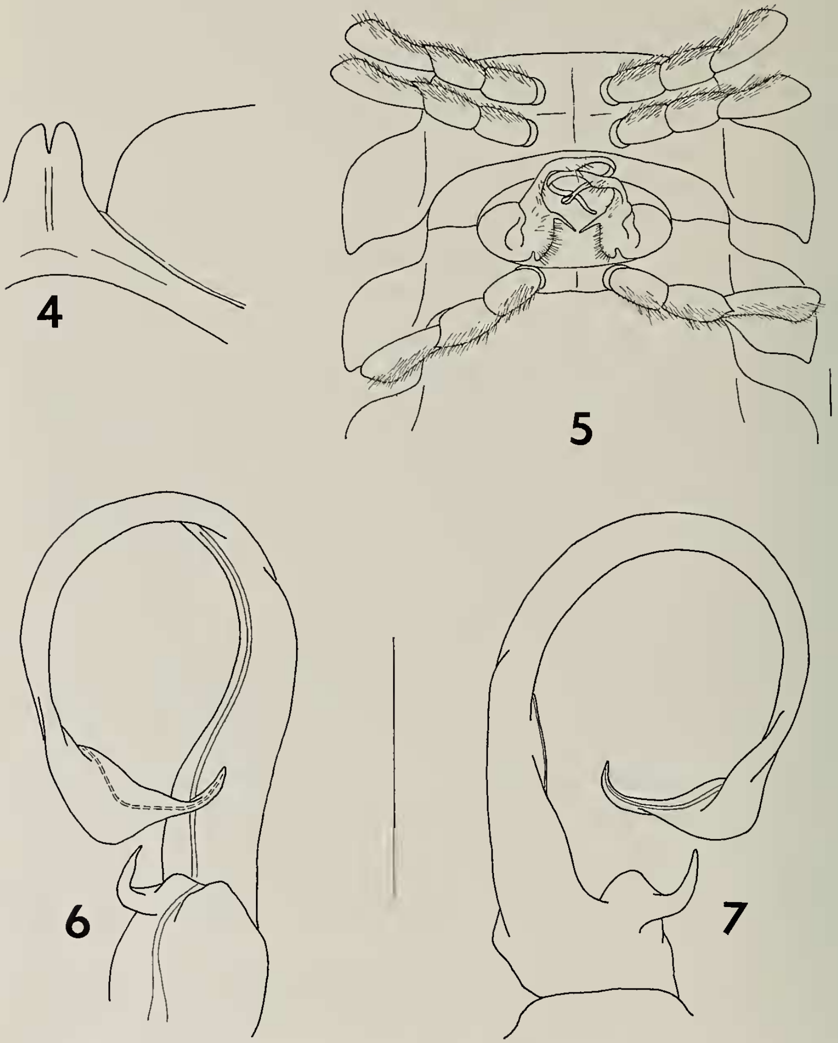
VIRGINIA. — *Giles Co.,* Mountain Lake Biological Station, M, July 1942, A.C. Cole (RVC) and M, F, June 1947, H.H. Hobbs et al. (NMNH).

Sigmoria (Rudiloria) guyandotta (Shear), new combination Figs. 8-9

Apheloria guyandotta Shear, 1972:494-496, Figs. 1-2.

Type specimens. — Male holotype (MCZ) and six male and two female paratypes (WAS) collected by P. Vogel and M. McGraw, 28 May-1 June 1968, from Shaft Hollow near McGraws, Wyoming Co., WV.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange extending from distal portion of basal zone to midlength of peak and with yellow paranota and red or red-orange middorsal spots, latter tending to



FIGS. 4-7. *Sigmoria (Rudiloria) trimaculata kleinpeteri.* 4, process of 4th sternum of male from Washington Co., VA, caudal view. 5, gonopods *in situ,* ventral view of the same. 6, telopodite of left gonopod of the same, medial view. 7, the same, lateral view. Scale line for fig. 5 = 1.00 mm; line for other figs. = 1.00 mm for each.

form diffuse or distinct metatergal stripes; gonopods with following diagnostic characters: prefemoral process absent; acropodite moderately thick, arch leaning anteriomediad and extending well beyond level of prefemur; basal zone short, inner surface directed mediad; anterior bend poorly defined; peak relatively long, sides narrowing with highest point distad; apical curve well defined; distal zone moderately long, coplanar with basal zone, directed nearly ventrad from peak, flared for entire length with lamellae on both sides, narrowing distad to acuminate tip; medial flange narrow and inconspicuous in medial view; lateral flange narrow and indistinct.

Color in Life. — Variable within species and individuals. According to Shear (1972) the paranota are yellow and the metaterga are black with red or red-orange median spots that may or may not form distinct or diffuse stripes along the caudal edges connecting with the paranotal spots. The collum of the holotype has an anteriomedian red spot with a diffuse yellow stripe along the caudal margin.

Holotype. — The following descriptions of the pregonopodal sterna and the gonopods in "sigmoid" terminology are supplemental to the more complete description by Shear (1972).

4th sternum with small, divided lobe, much shorter than widths of adjacent coxae (Fig. 8); 5th sternum with minute, barely detectable elevations between anterior legs, flat and unmodified between posterior legs; 6th sternum flattened, without depression on caudal edge.

Gonopods *in situ* (see Shear, 1972, Fig. 1) with acropodites extending mediad across midline, lying one in front of other, curving dorsad over opposite side and inserting on opposite prefemur. Gonopod structure as follows (Fig. 9): Prefemoral process absent. Acropodite moderately thick, arch leaning anteriomediad, overhanging and extending well beyond level of prefemur; basal zone relatively short, with inner surface directed mediad; anterior bend moderately broad, poorly defined; peak relatively long, rising continuously to apex at distal extremity, sides narrowing distad; apical curve broad but well defined; distal zone moderately long, coplanar with basal zone, directed nearly ventrad from peak, flared for entire length with lamellae on both sides, narrowing and curving distad to subacuminate tip. Medial flange long and narrow, indistinct, terminating and blending into inner margin of peak distal to midlength. Lateral flange short, narrow, and inconspicuous, located on distal zone opposite ventral bend. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Shear (1972) briefly described somatic features.

Cyphopods *in situ* with receptacles visible in aperture, valves directed dorsad. Receptable large, hood-like, enveloping valves, surface rugulose. Valves small, equal, surfaces finely granulate.

Variation. — The male from Menifee County, Kentucky, has a small, acute, nubbinlike prefemoral process.

Ecology. — Unknown.

Distribution. — Known from two small, allopatric populations in southern West Virginia and east-central Kentucky. Comparatively little sampling has taken place in eastern Kentucky, however, and *guyandotta* should occur in the intervening area. Material was examined from the following new localities:

KENTUCKY. — *Rowan Co.,* Moreland, M, 14 July 1961, A Razor (FSCA). *Menifee Co.,* 4.5 mi. NE Slade, Dunkan Hollow, M, 3F, 31 August 1957, L. Hubricht (RLH).

Remarks. — Except for being flared, the distal zone of *guyandotta* has the same basic configuration as that of *mohicana,* and the rounded lobe on the outer margin at the apical curve and the beginning of the flare appears homologous to the lobe in that position in *mohicana.* Though more pronounced, the lobes on the distal zone in *t. kleinpeteri,* when examined from the ventral perspective, have a similar configuration to the flange of *guyandotta.* However, the distal zone of *guyandotta* is shorter than that of *t. kleinpeteri,* the flanges are smaller, and the portion distal to the flanges is absent. Thus, the acropodite of *guyandotta* is intermediate between those of *t. kleinpeteri* and *mohicana,* and the forms may be clinally continuous and conspecific. A final decision on their statuses is left to future investigators with access to more material from uncollected areas in Kentucky, West Virginia, and Ohio.

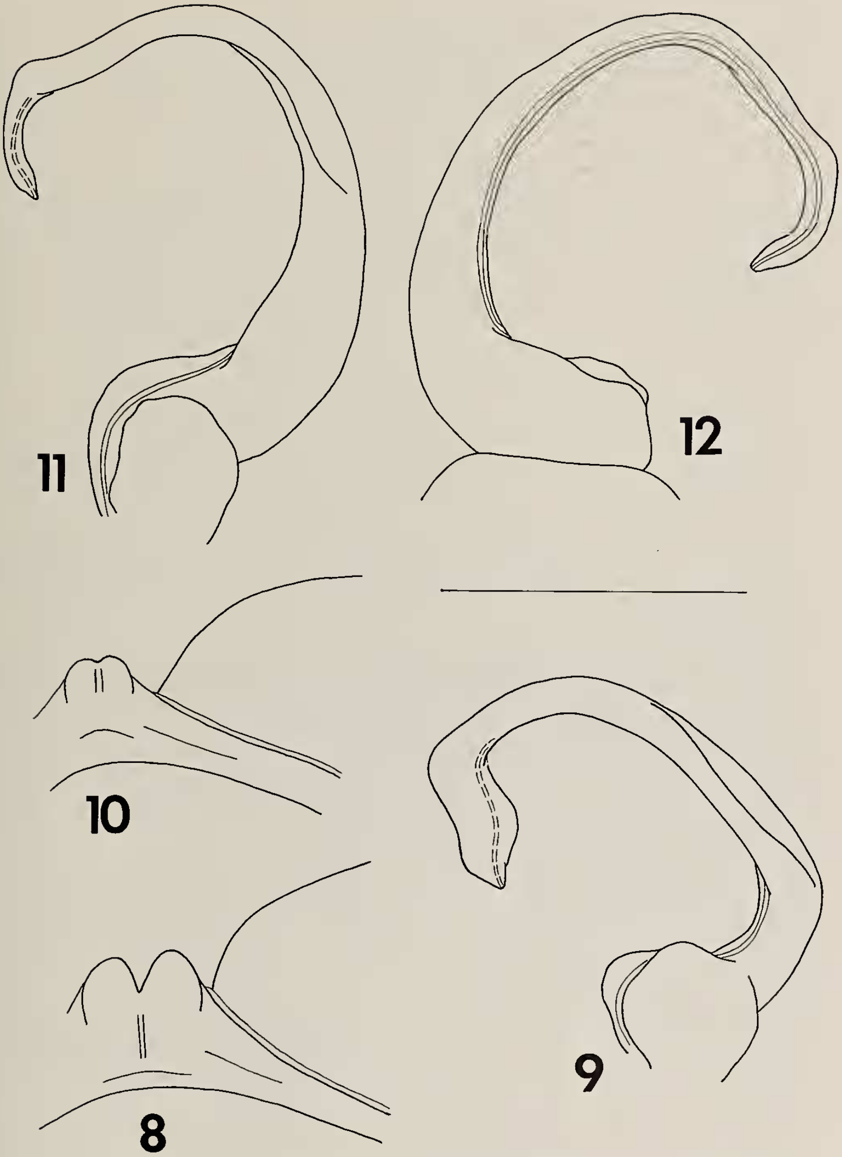
Sigmoria (Rudiloria) mohicana (Causey), new combination Figs. 10-12

Fontaria trimaculata (nec Wood): Williams and Hefner, 1928:108-109, Fig. 10c.
Rudiloria mohincana Causey, 1955:28-29, Fig. 6.
Rudiloria mohicana: Chamberlin and Hoffman, 1958:47. Hoffman, 1978, Fig. 4.
Apheloria mohicana: Shear, 1972:496-497, Fig. 3.

Type specimens. — Male holotype (AMNH) collected by L. Gray, August 1951, from Mohican State Park, Ashland Co., OH. There are no paratypes.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange extending from distal extremity of basal zone to midlength of peak and with metatergal stripe color pattern; gonopods with following diagnostic characters: prefemoral process absent; acropodite thin and fragile, arch high and rounded, extending beyond level of prefemur; basal zone with inner surface directed mediad; anterior bend poorly defined; peak gently rounded; apical curve with two broad bends; distal zone moderately long, directed laterad from peak, not coplanar with other sections, widest basally with slight proximal lobe on outer margin, tapering to acuminate tip; medial flange narrow and inconspicuous; lateral flange absent.

Color in Life. — Unknown. Causey (1955) described the color pattern after two years in alcohol, and although the pigments had disappeared, the striped pattern was evident. It still is



FIGS. 8-12. 8-9, *Sigmoria (Rudiloria) guyandotta*. 8, process of 4th sternum of holotype, caudal view. 9, telopodite of left gonopod of the same, medial view. 10-12, *Sigmoria (Rudiloria) mohicana*. 10, process of 4th sternum of holotype, caudal view. 11, telopodite of left gonopod of holotype, medial view. 12, the same, lateral view. Scale line = 1.00 mm for 10-12; 1.14 mm for 8-9.

today after 30 years of preservation, and there are broad stripes along the caudal margins of the metaterga and both edges of the collum.

Holotype. — The following account of the pregonopodal sterna and the gonopods in "Sigmoid" terminology supplements previous descriptions by Causey (1955) and Shear (1972). 4th sternum with small, undivided lobe, much shorter than widths of adjacent coxae (Fig. 10); 5th sternum with slight elevations between 4th legs and smaller ones between 5th legs; 6th sternum flat, without depression in caudal edge.

In situ arrangement of gonopods unknown. Gonopod structure as follows (Figs. 11-12): prefemoral process absent. Acropodite thin and fragile, forming high arch, gently and unevenly rounded, overhanging and extending beyond level of prefemur; basal zone relatively long, inner surface directed mediad, without modifications; anterior bend broad, poorly defined; peak gently rounded, highest proximal to midlength; apical curve with two broad bends; distal zone moderately long, curving laterad from peak, not coplanar with basal zone, with two bends, widest basally with slight proximal lobe on outer margin, sides narrowing and tapering smoothly to subacuminate tip. Medial flange narrow and inconspicuous, arising near anterior bend, terminating by blending into inner margin of peak near midline, without lobes. Lateral flange absent, possibly represented by slight lobe on outer margin at proximal corner of distal zone. Prostatic groove crossing to lateral surface on basal zone, continuing to terminal opening.

Distribution. — Known from the type locality and probably also Marietta, Washington County, and Athens, Athens County, Ohio (Williams and Hefner 1928).

Remarks. — The acropodite of *mohicana* is convergent with forms of *nigrimontis intermedia (Sigiria)* in its thin, fragile structure, the double bend in the distal zone, and the apical configuration (see Shelley 1981a, Figs. 114-121, p. 114). Also noteworthy is the laterally directed distal zone, which is not coplanar with the basal zone. This feature is less pronounced than that in species of *Falloria* in the Cumberland Plateau of Tennessee, which occur nearly due south of *mohicana.*

Thirty years after its discovery, the type specimen is still the only authentic individual of *mohicana.* Thus, nothing can be said about variation, female anatomy, and ecological preferences since the habitat was not indicated in the original description. This one male is also the only authentic specimen of *Sigmoria s. lat.* from the state of Ohio, which can be expected to have a wealth of forms because the type locality is in the north-central part, about 60 miles south of Lake Erie. I agree with Shear (1972) that *mohicana* probably occurs throughout the hill country of southern Ohio, and one of the remaining needs in the study of *Sigmoria s. lat.* is more material from this state and adjacent parts of West Virginia and Kentucky.

I include under *mohicana* the records of *Fontaria trimaculata* from Athens and Marion, Ohio, published by Williams and Hefner (1928). Their species was probably not *corrugata,* for which they reported a different color pattern and which they claimed was abundant in this section of Ohio.

The gonopod drawings are adjacent, and although from different angles, appear to be of different forms. Hoffman (1951) also reported seeing a new genus and species from Ohio that had been sent to him by Hefner[7] and suggested that it was the same as Williams and Hefner's form. Their drawing of "*trimaculata*" shows a moderately slender, symmetrically curved acropodite with a slightly greater apical curve directed inward into the arch. *Sigmoria (R.) mohicana* appears like this from certain perspectives, and there is a notable similarity between the figure of Williams and Hefner and that of *mohicana* published by Shear (1972, Fig. 3). The absence of a prefemoral process from Williams and Hefner's form also corresponds to the condition in *mohicana.*

Sigmoria (Rudiloria) rigida Shelley, new species Figs. 13-16

Type specimens. — Male holotype (RLH) and one male and three female paratypes collected by L. Hubricht, 16 June 1956, on Elk River bluffs, 1-1.5 mi. S Clay, Clay Co., WV. One male and three female paratypes (RLH) taken by same collector at same locality, 28 May 1952.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange located on distal portion of basal zone and with metatergal stripe color pattern; gonopods with following diagnostic characters: prefemoral process varying from small nub to small, triangular structure; acropodite thin and fragile, arch flattened and extending beyond level of prefemoral process; basal zone relatively long, inner surface directed mediad; anterior bend well defined; peak long, flattened, edges generally parallel; apical curve with two bends; distal zone moderately long, coplanar with basal zone, linear basally, bending into arch at 2/3 length, widening slightly then narrowing to acuminate tip; medial flange narrow and indistinct in medial view; tooth present at midlength of peak, rigid and spiniform; lateral flange absent.

Color in Life. — Unknown. Preserved material shows a clear pattern of stripes along the caudal margins of the metaterga connecting the paranotal markings and along both the anterior and posterior edges of the collum.

Holotype. — Length 34.5 mm, maximum width 7.9 mm, W/L ratio 22.9%, depth/width ratio 63.3%. Segmental widths as follows:

collum 6.4 mm	16th 7.3
2nd 7.0	17th 6.7
3rd 7.7	18th 5.2
4th-15th 7.9	

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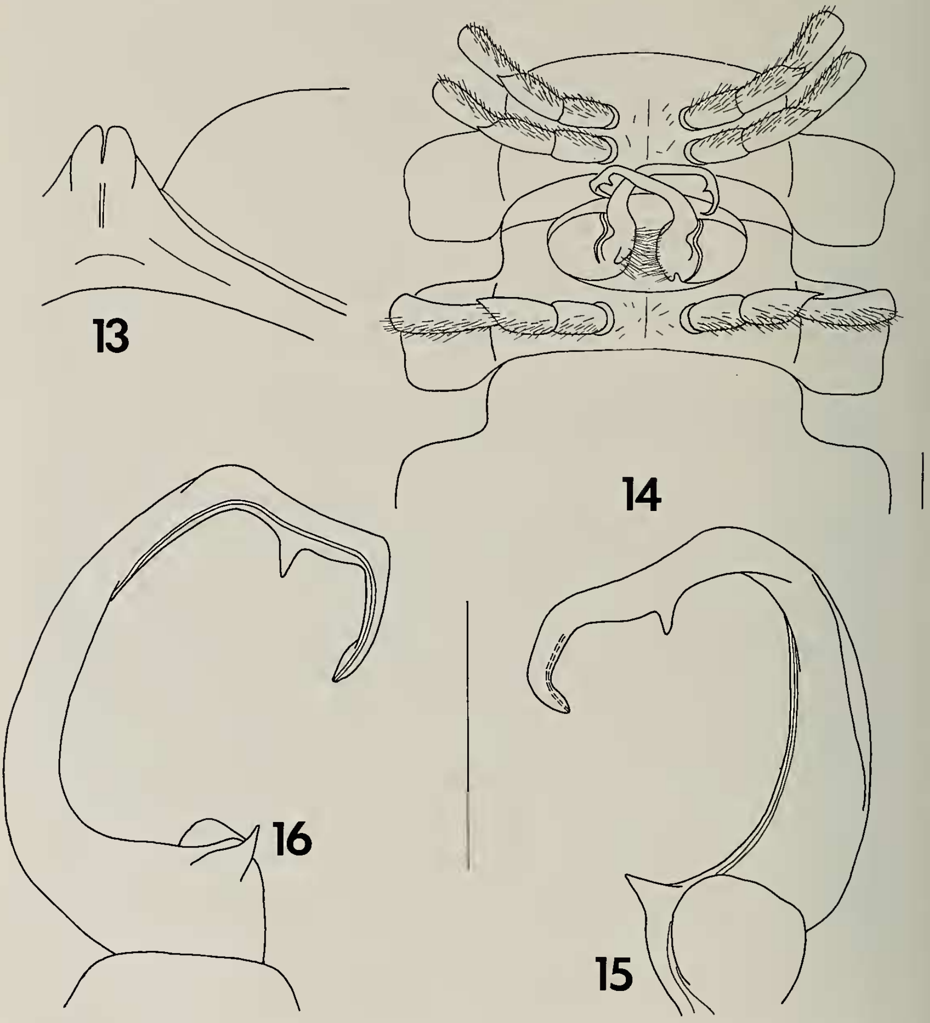
[7] This sample, from Marietta, Ohio, is present in Dr. Hoffman's collection, but the gonopods are lost and its assignment to *mohicana* needs confirmation.

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.3 mm, interantennal isthmus 1.5 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2 > 3 > 4 = 5 = 6 > 1 > 7. Genae without impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 10-10, labral 12-12.



Figs. 13-16. *Sigmoria (Rudiloria) rigida.* 13, process of 4th sternum of holotype, caudal view. 14, gonopods *in situ,* ventral view of paratype. 15, telopodite of left gonopod of holotype, medial view. 16, the same, lateral view. Scale line for fig. 14 = 1.00 mm; line for other figs. = 1.00 mm for each.

Dorsum smooth, polished, becoming moderately coriaceous on anterior half of paranota. Collum moderately broad, ends broadly rounded and extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 8, blunt on 9-14, becoming progressively more acute posteriorly. Peritremata thin but distinct, moderately elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum apically divided, shorter than widths of adjacent coxae (Fig. 13); 5th sternum with two paramedian knobs between anterior legs, shorter than widths of adjacent coxae, and broad elevated area between caudal legs; 6th sternum flat, without convex recessions in caudal edge. Postgonopodal sterna flat and plate-like, with slight bicruciform impressions on 8 and 9. Coxae with small tubercles beginning on segment 12, becoming progressively larger posteriorly; prefemoral spines arising on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 2.7 mm wide and 1.5 mm long at midpoint, without indentations, sides flush with metazonal surface. Gonopods *in situ* (Fig. 14, of paratype) with acropodites extending mediad across midline, lying one in front of other, curving dorsad over opposite side and touching opposite coxa. Gonopod structure as follows (Figs. 15-16): Prefemoral process small, triangular, directed toward tip of acropodite; prefemur with small, acute spur on medial surface at juncture with basal zone, spur obscured in medial view. Acropodite relatively thin and fragile, forming high, flattened arch, overhanging and extending beyond level of prefemoral process; basal zone relatively long, inner surface directed mediad, without modifications; anterior bend sharp, well defined; peak moderately long, flattened, edges parallel with slight concavity on outer margin; apical curve in two parts, a broad, proximal curve followed by a linear section then a sharp distal curve; distal zone moderately long, coplanar with basal zone, with a linear basal portion bent abruptly into arch at 2/3 length, widening slightly apically then narrowing rapidly to subacuminate tip; latter directed toward prefemur. Medial flange narrow and indistinct, located entirely on basal zone, barely detectable in medial view. Tooth present, a short, rigid spiniform projection at midlength of peak. Lateral flange absent. Prostatic groove crossing to lateral side proximal to anterior bend, continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Badly fragmented and unmeasurable. Cyphopods *in situ* with openings of valves visible in aperture. Receptacle moderate, located anteriomediad to valves, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — Males from Kanawha and Nicholas counties have only a small nubbinlike prefemoral process, and the tooth is slightly shorter and more rounded apically.

Ecology. — Unknown.

Distribution. — Known only from a small triangular area between US highways 19 and 119 in the Elk and Gauley River drainages in central West Virginia. Material was examined as follows:

WEST VIRGINIA. — *Kanawha Co.,* 0.5 mi. N Falling Rock, Elk R. bluffs, M, 28 May 1952, L. Hubricht (RLH). *Clay Co.,* 1-1.4 mi. S Clay, Elk R. bluffs, M, 3F, 28 May 1952, and 2M, 3F, 16 June 1956, L. Hubricht (RLH) and M, F, 7-9 September 1958, MacMillan and Richmond (RLH). TYPE LOCALITY. *Nicholas Co.,* 4 mi NE Swiss, M, 2 September 1965, R.L. Hoffman (RLH).

Remarks. — Similarities between *rigida* and *stenogon/nantahalae (Sigiria/Falloria),* some 240 miles south in southwestern North Carolina are worth noting. The tooth arises suddenly at midlength of the peak, just as in *nantahalae,* and the double bend in the distal zone is similar to that in *stenogon,* although the latter is somewhat bisinuate.

The only differences between *rigida* and *mohicana* are the tooth (present in *rigida,* absent in *mohicana*), the prefemoral process (present in *rigida,* absent in *mohicana*), and a slightly higher and more rounded arch in

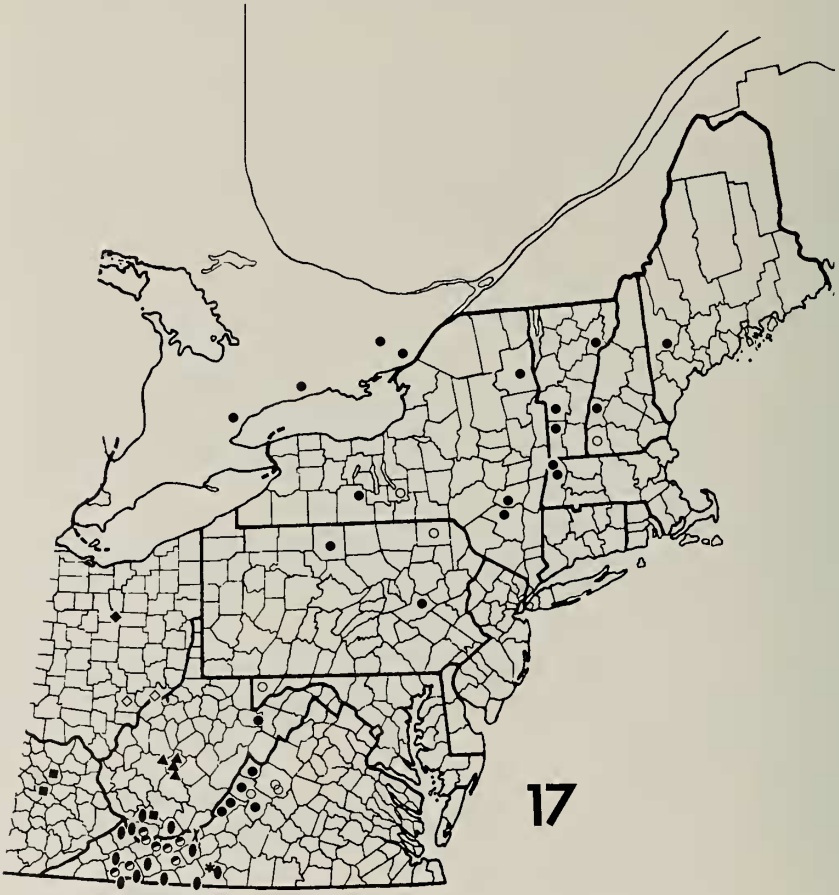


Fig. 17. Distribution of species of *Sigmoria* from Virginia northward, excepting the subgenus *Dixioria.* Ovals, *l. latior;* dots, *t. trimaculata;* half shaded dots, *t. kleinpeteri;* X, *trimaculata* intergrades; squares, *guyandotta;* triangles, *rigida;* diamonds, *mohicana;* asterisk, *whiteheadi.* Open symbols indicate literature records believed to be reliable.

mohicana. The two are thus closely related and may eventually be shown to be subspecies. The hypothesized connection between *t. kleinpeteri, guyandotta,* and *mohicana* may therefore continue eastward and include *rigida*. If so, *Rudiloria* will contain only one species, and the forms will connect in a spiral configuration that curls inward and terminates centrally.

SIGMORIA (DIXIORIA) Chamberlin, new status

Dixioria Chamberlin, 1947:28. Hoffman, 1956a:6-7; 1979:158. Chamberlin and Hoffman, 1958:31. Jeekel, 1971:259.

Type species. — *Dixioria dentifer* Chamberlin, 1947, by original designation.

Diagnosis. — Color pattern constant, paranota yellow, metaterga uniformly black, collum with concolorous yellow stripe along anterior margin; caudolateral corners of paranota rounded through midbody segments; gonopods *in situ* with acropodites extending mostly over opposite side of aperture and inserting beside opposite coxa, perhaps with sides leaning over anterior margin but apices not projecting over latter nor between legs of segment 6; acropodites relatively thin and fragile, without flanges; tooth usually present, located on peak or distal zone; smaller accessory tooth usually present, arising from undersurface of acropodite at or distal to level of tooth; tip simple.

Remarks. — The subgenus *Dixioria* occupies a roughly triangular area in the contiguous corners of North Carolina, Tennessee, and Virginia. The northernmost known locality is in Tazewell County, Virginia, and the Nolichucky River in North Carolina and Tennessee forms a sharp southern distributional limit. The cove dwelling species of the other subgenera do not occur north of this watercourse and are replaced by *Dixioria*. The only sympatric congeners are *latior (Sigmoria)* and *t. kleinpeteri (Rudiloria),* the former being an ecological generalist and thus able to occur outside coves.

The subgenus *Dixioria* is distinguished by both somatic and gonopodal features. The caudolateral corners of the paranota are distinctly rounded over the anterior 2/3 of the body, and even the caudalmost are apically blunt rather than acute. In all other species groups, the caudolateral corners are rounded only through about segments 5-7, after which they become blunt and progressively more acute caudally to around segment 15. Thus, females as well as males can be accurately placed in *Dixioria* on the basis of this diagnostic trait. As in the subgenus *Rudiloria* the gonopods *in situ* extend more mediad than anteriad, projecting over the opposite side of the aperture and often curving dorsad so that the distal zone of one acropodite touches the coxa of the other. The gonopods are characterized by large prefemoral processes and relatively thin, fragile acropodites. A variable tooth is usually present on the distal extremity of the peak or proximal half of the distal zone, and the forms lacking it have a slightly expanded, rounded medial margin there. Medial and lateral flanges are absent. Six of the seven species display a smaller and sharply acute accessory tooth, which arises from the undersurface of the acropodite at or distal to the level of the main, marginal, tooth. This accessory tooth also is diagnostic for *Dixioria.*

Hoffman (1956a) revised this assemblage, recognizing two species, one with six subspecies. Here I synonymize one subspecies and elevate the others to specific rank. Although the true relationship of *acuminata* to both *pela* and *coronata* in Tennessee remains to be settled, enough collecting has taken place in North Carolina to show that *pela, wrighti,* and *coronata* are not linked by intergrades as in *latior (Sigmoria).* All have sharp distributional boundaries and are therefore considered reproductively isolated, and a new species exists between *wrighti* and *coronata.* As brief descriptions were previously provided by Hoffman (1949, 1956a), I describe only *pela, brooksi, dactylifera,* and the new species. Supplemental accounts, describing the process of the 4th sternum and the gonopods in "sigmoid" terminology, are provided for the others. *Dixioria* consists of a single species group, the *pela* group.

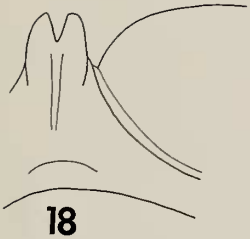
Components. — pela (Chamberlin), *acuminata* (Hoffman), *coronata* (Hoffman), *wrighti* (Hoffman), *watauga* new species, *brooksi* (Hoffman), *dactylifera* (Hoffman).

Sigmoria (Dixioria) pela (Chamberlin), new combination Figs. 18-24

Fontaria pela Chamberlin, 1918b:122-123. Attems, 1938:167.
Dixioria dentifer Chamberlin, 1947:28-29, Fig. 13.
Dixioria pela pela: Hoffman, 1956a:8-11, Fig. 1a. Chamberlin and Hoffman, 1958:31.
Apheloria pela: Wray, 1950:44; 1967:44.

Type specimens. — Male and female paratypes (RLH, MCZ) collected by R. Thaxter in July of unknown year at Burbank, Carter Co., TN. The holotype is missing from the latter repository where both Hoffman (1956a)

FIGS. 18-24. *Sigmoira (Dixioria) pela.* 18, process of 4th sternum of paratype caudal view. 19, gonopods *in situ,* ventral view of male from Mitchell Co., NC. 20, telopodite of left gonopod of paratype, medial view. 21, the same, lateral view. 22, telopodite of left gonopod of another paratype, medial view. 23, distal zone of male from 3.8 mi. SE Poplar, Mitchell Co., NC, medial view. 24, the same of male from 3.8 mi. SE Spruce Pine, Mitchell Co. Scale line for fig. 49 = 1.00 mm; line for other figs. = 1.00 mm for 23-24, 1.25 mm for 22, 1.43 mm for 18 and 21, and 1.66 mm for 20.



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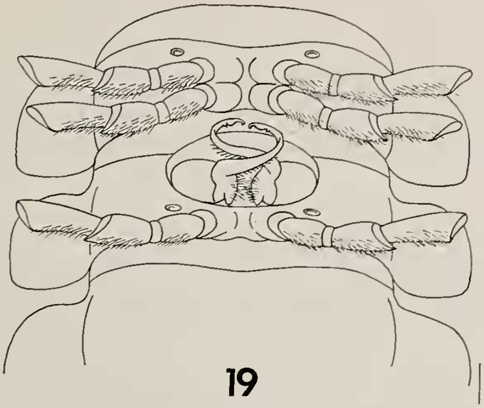

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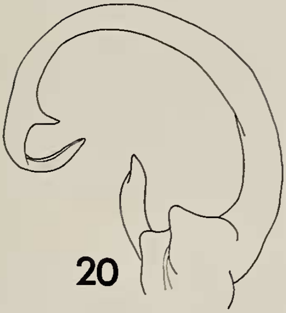

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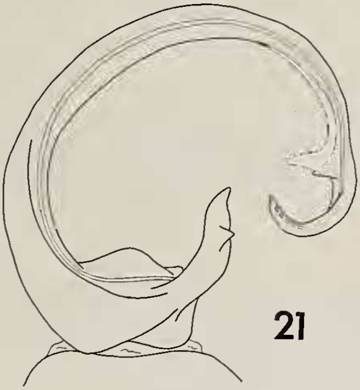

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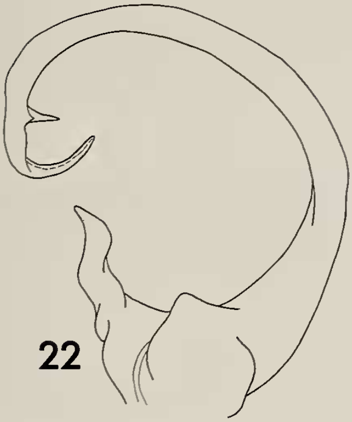

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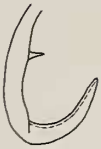

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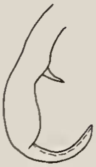

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and Chamberlin and Hoffman (1958) report its deposition. It may be among the Chamberlin material now being accessioned by the NMNH.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, thick, and variably straight, curved, or bisinuate; acropodite thin and fragile, configuration a broad, smooth, continuous curve forming nearly complete circle with prefemoral process; anterior bend and apical curve broad, poorly defined; peak gently curved, apex near midlength; distal zone long, curving broadly dorsad and bending abruptly inward into arch distal to midlength; tooth present or absent, distomedial margin of distal zone slightly expanded and gently rounded when present, not expanded when absent, tooth located proximal to midlength of distal zone, length and configuration variable; accessory tooth present, arising from inner surface of distal zone at level of tooth, variably triangular to spiniform; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Male Paratype. — Length 35.0 mm, maximum width 7.2 mm, W/L ratio 20.6% depth/width ratio 68.0%. Segmental widths as follows:

collum	5.5 mm	14th-15th	7.0
2nd	6.7	16th	6.1
3rd-12th	7.2	17th	5.2
13th	6.8	18th	4.8

Somatic features as in *l. latior,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.6 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres $2>3>6>4=5>1>7$. Genae with distinct central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 8-8, labral about 12-12.

Dorsum finely granulate, becoming smooth and polished on paranota, with very little wrinkling. Collum broad, ends not extending beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 11, blunt on 12-14, becoming progressively more acute posteriorly. Peritremata flat and indistinct, slightly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with moderate process between 3rd legs, length equal to widths of adjacent coxae (Fig. 18); that of segment 5 with two low, medially coalesced knobs between 4th legs, much shorter than widths of adjacent coxae, and rounded, elevated areas between 5th legs; that of segment 6 with convex recession between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on segments 8-10 and variably broad, shallow, central impressions on remaining segments. Coxae with low, blunt tubercles arising on segment 9, becoming progressively longer and sharper caudally; prefemoral spines arising on segment 5, becoming progressively longer and more acute posteriorly.

Gonopodal aperture ovoid, 3.5 mm wide and 1.8 mm long at midpoint, without indentations, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 19, not this specimen) with acropodites projecting mediad and crossing each other in midline, curving broadly over opposite side of aperture then back toward midline, extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 20-21): prefemoral process a moderately long, upright peg-like projection, directed toward peak and extending beyond level of tip of acropodite, of nearly equal width throughout, narrowing apically, with distal spur on lateral side. Acropodite relatively thin and fragile, configuration a smoothly curved arch overhanging and extending well beyond level of prefemoral process; basal zone moderately long and gently curved, without modifications; anterior bend broad, poorly defined, continuous with apical curve through peak; peak gently curved, apex at midlength; apical curve broad, poorly defined; distal zone long, projecting laterad from peak and not coplanar with basal zone, bending abruptly into arch distal to midlength and tapering to blunt tip; latter directed toward anterior bend. Medial and lateral flanges absent. Tooth moderately long, triangular, and apically subacuminate, located distal to midlength of distal zone; accessory tooth shorter, triangular, and apically acute, located at same position and obscured in medial view. Prostatic groove crossing to lateral side on prefemur and continuing to terminal opening.

Other Male Paratypes. — The type males vary more than those in any other sample. The prefemoral process varies from bisinuate to gently curved, and the arch of the acropodite extends to the level of the prefemoral process in some individuals and well beyond the latter in others. The tooth varies from distinct and sharply triangular to a small, rounded vestige, and the distal zone is slightly wider and has a gently curved medial edge distal to the teeth in the latter condition (Fig. 22).

Female Paratype. — Length 37.6 mm, maximum width 8.7 mm, W/L ratio 23.1%, depth/width ratio 65.5%. Agreeing closely with males in somatic features except coxal tubercles more sharply acute. Cyphopods *in situ* with sides of receptacles visible in aperture, valves directed laterad. Receptacle moderately large, cupped around medial ends of valves, surface rugulose. Valves moderate, equal, surface finely granulate.

Variation. — Variation in the prefemoral process is as described for paratypes, but most individuals resemble the bisinuate condition. On the acropodites the arch is broader in some males, and the great majority lack the tooth. In these the accessory tooth is visible in medial view (figs. 23-24). About half of the available males have an expanded, rounded distomedial margin of the distal zone (Fig. 23), and about half have a narrow, linear edge (Fig. 24). There is no detectable geographic pattern to the distributions of these two forms.

Ecology. — Sigmoria (D.) pela is a cove dwelling species. As stated previously by Shelley (1981a), the mountains in northwestern North Carolina north of the Nolichucky-Toe Rivers are more segregated from each other and have fewer ridges and clusters of peaks than those south of this boundary. Consequently, cove environments are rarer, and most forms of *Dixioria* are found along streams under thin layers of leaves on relatively hard substrates.

Distribution. — Sigmoria (D.) pela spans the Blue Ridge Province immediately north of the Nolichucky River, from near the escarpment in McDowell-Burke counties, North Carolina, to western Carter County, Tennessee, near the boundary with the Ridge and Valley Province. I have collected extensively south of the Nolichucky and can confirm Hoffman's prediction (1956a) that it forms the southern distributional limit. The range is only two counties wide in each state, and the northern limit does not correspond to any particular physiographic feature. Material was examined as follows:

TENNESSEE. — *Carter Co.,* 1 mi. NW Hampton, Doe River bluff, M, F, 3 May 1951, L. Hubricht (RLH); and Burbank, MM, FF, complete date unknown, R. Thaxter (MCZ, RLH) TYPE LOCALITY. *Unicoi Co.,* 3 mi. E Erwin, co. rd. 2457 at Rock Creek Rec. Area, Cherokee Nat. For., 2M, F, 20 May 1978 (NCSM A1973).

NORTH CAROLINA. — *Avery Co.,* 4.4 mi. N Elk Park, along co. rd. 1305, 1.7 mi. N jct. co. rd. 1307, 2M, 8 September 1973 (NCSM 1999); 2.8 mi. N Elk Park, Elk Falls on co. rd. 1305, M, 29 October 1977 (NCSM A1774); Cranberry, M, 2F, June 1896, A. Wenzell (ANSP); 4 mi. N Newland, along US hwy, 19E, 0.8 mi. S. jct. co. rd. 1168, M, F, 20 June 1980 (NCSM A3323); 6.5 mi. W Newland, along co. rd. 1130, 0.8 mi. W. jct. US hwy. 19E, 3M, 2F, 20 June 1980 (NCSM A3320); and 4 mi. S Newland, along co. rd. 1143, 1.7 mi. NW jct. US hwy. 221, 3M, 20 June 1980 (NCSM A3324). *Mitchell Co.,* 12 mi. NW Bakersville, along co. rd. 1320, 0.7 mi. N jct. co. rd. 1321, 0.8 mi. N jct. co. rd. 1320, 5M, F, 24 July 1975 (NCSM A409); 1.5 mi. N Poplar, along co. rd. 1323, 2.1 mi. N jct. co. rd. 1321, M, 21 May 1978 (NCSM A1976); 11 mi. N Spruce Pine, along NC hwy 261, 0.1 mi. W jct. co. rd. 1159, M, 21 June 1980 (NCSM A3325); 3 mi. NW Spruce Pine, along co. rd. 1164, 0.5 mi. W jct. co. rd. 1162, 2M, 2F, 21 June 1980 (NCSM A3331); and 3.8 mi. SE Spruce Pine, along co. rd. 1129, 0.4 mi. N jct. co. rd. 1128, 2M, 24 June 1975 (NCSM A408). *McDowell-Burke cos.* — county line on US hwy. 221, 3F, 22 June 1980 (NCSM A3332).

Remarks. — The female only sample from the last locality is tentatively assigned to *pela,* the only proximal species.

The holotype of *D. dentifer,* said by Hoffman (1956a) and Chamberlin and Hoffman (1958) to be at the AMNH, is actually at the ANSP.

Sigmoria (Dixioria) acuminata (Hoffman), new combination, new status

Figs. 25-27

Dixioria pela acuminata Hoffman, 1956a:11-12, Fig. 1b.

Type specimen. — Male holotype (NMNH) collected by J.A. Fowler and R.L. Hoffman, 19 June 1950, from Johnson Co., TN, at the summit of Holston Mountain, 2 mi. W of Shady Valley. There are no paratypes.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, thick, and

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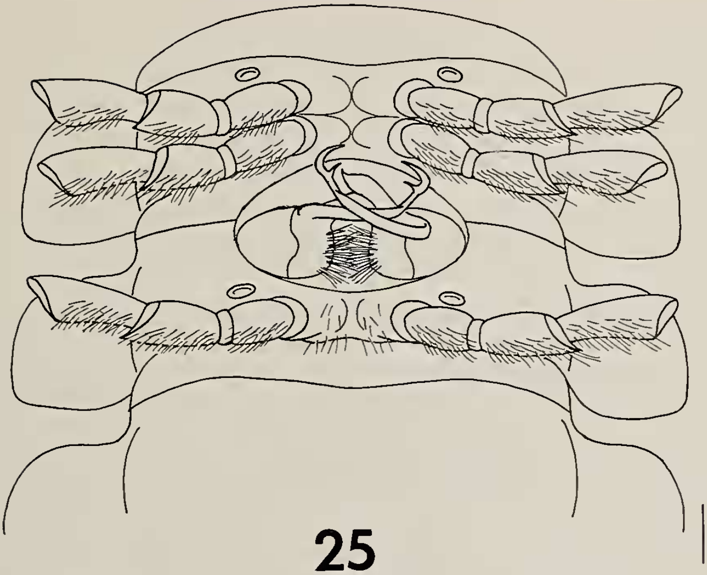
FIGS. 25-27. *Sigmoria (Dixioria) acuminata.* 25, gonopods *in situ,* ventral view of holotype. 26, telopodite of left gonopod of holotype, medial view. 27, distal zone of the same, lateral view. Scale line for fig. 25 = 1.00 mm; line for other figs. = 1.00 mm for each.



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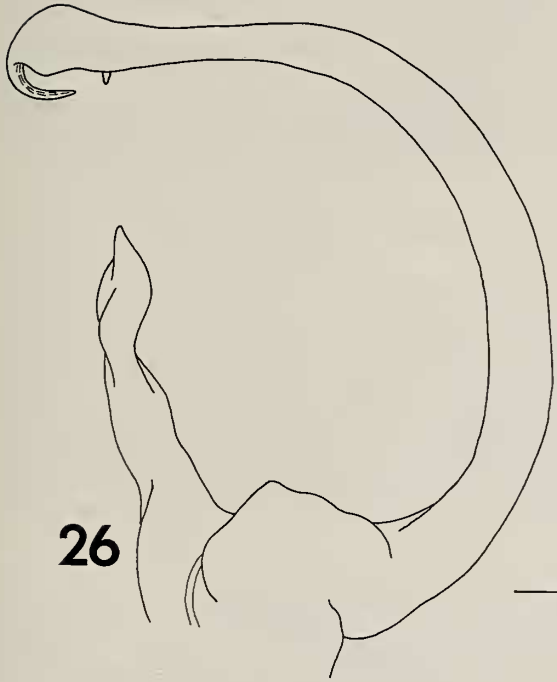

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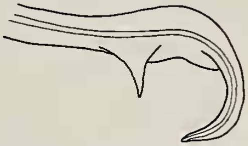

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curved; acropodite thin and fragile, configuration a flattened, open arch; anterior bend broad, poorly defined; peak flattened and linear with distal margins slightly expanded and gently rounded; apical curve sharp, well defined; distal zone short, bending sharply into arch, lying parallel to and beneath distal extremity of peak; tooth absent; accessory tooth present, located distad on peak; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae.

Gonopods *in situ* (Fig. 25) with acropodites projecting mediad and crossing each other in midline, curving broadly over opposite side of aperture and extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 26-27): prefemoral process moderately long, upright, indented and curving slightly near midlength, tapering distad to subacuminate tip, directed toward peak. Acropodite relatively thin and fragile, configuration a flattened, open arch extending just beyond level of prefemoral process; basal zone moderately long, gently curved, without modifications; anterior bend broad, poorly defined; peak flattened, linear, distal margins slightly expanded and rounded; apical curve sharp, well defined; distal zone short, not coplanar with basal zone, curving sharply into arch and lying parallel to and beneath distal extremity of peak; tip acuminate. Tooth and medial and lateral flanges absent. Accessory tooth present, arising from inner surface of peak at level of expanded medial margin. Prostatic groove crossing to lateral side on prefemur and continuing to terminal opening.

Variation. — The male from the second locality agrees closely with the holotype.

Distribution. — Known only from Holston Mountain in western Johnson County, Tennessee. The following specimen was examined in addition to the holotype:

TENNESSEE. — *Johnson Co.,* 3 mi. S Shady Valley, along TN hwy. 91, M, 17 May 1964, R.L. Hoffman (RLH).

Remarks. — This is the westernmost form of *Dixioria.* Its true status awaits more sampling in southern Johnson and northern Carter counties, Tennessee, and it might be a subspecies of *pela,* forms of which also lack the tooth and have a slightly expanded distomedial margin of the peak. As Holston Mountain is near the western periphery of the Blue Ridge Province, future investigators should also look for *acuminata* in the adjacent Ridge and Valley Province. Just as *coronata* occurs in this region farther north, *acuminata* may inhabit it on the western side of the subgeneric range.

Sigmoria (Dixioria) coronata (Hoffman), new combination Figs. 28-31

Deltotaria coronata Hoffman, 1949:380-381, Pl. 26, Figs. 7-8.
Dixioria pela coronata: Hoffman, 1956a:12-13, Fig. 1c. Chamberlin and Hoffman, 1958:31.
Dixioria pela fowleri Hoffman, 1956a:13-14, Fig. 1e. **NEW SYNONYMY.**

Type specimens. — Male holotype, female allotype, and male paratype (NMNH) collected by H.I. Kleinpeter and R.L. Hoffman, 1 July 1947, from Mt. Rogers, Grayson Co., VA.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, variably curved to bisinuate; acropodite moderately thick and heavy, configuration a flattened, open arch; anterior bend broad, poorly defined; peak linear with margins essentially straight; apical curve sharp, well defined; distal zone short, curving gently into arch and nearly overlapping tooth; latter located on distal extremity of peak, apically rounded and moderately long, nearly equal in length to distal zone; accessory tooth present, arising from inner surface of peak beside base of tooth; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae.

Gonopods *in situ* (Fig. 28, ventral view of paratype) with acropodites projecting mediad and crossing each other near midlengths in midline, curving broadly over opposite side of aperture and extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 29-30): prefemoral process relatively long, upright, curving slightly into arch near midlength, apically blunt, directed toward tooth. Acropodite moderately thick and heavy, configuration a flattened, open arch extending to level of prefemoral process; basal zone moderately long, gently curved, without modifications; anterior bend broad, poorly defined; peak flattened and linear, margins straight; apical curve sharp, well defined; distal zone short, curving gently into arch and nearly overlapping tooth, not coplanar with basal zone; tip subacuminate. Medial and lateral flanges absent. Tooth moderately long, apically rounded, located distad on peak; accessory tooth shorter, triangular, and apically acute, located at same position and obscured in medial view. Prostatic groove crossing to lateral side on prefemur, continuing to terminal opening.

Variation. — The distal zone does not curve inward into the arch in northern males (Fig. 31). Otherwise, all gonopods agree closely with those of the holotype.

Ecology. — *Sigmoria (D.) coronata* is a cove dwelling species.

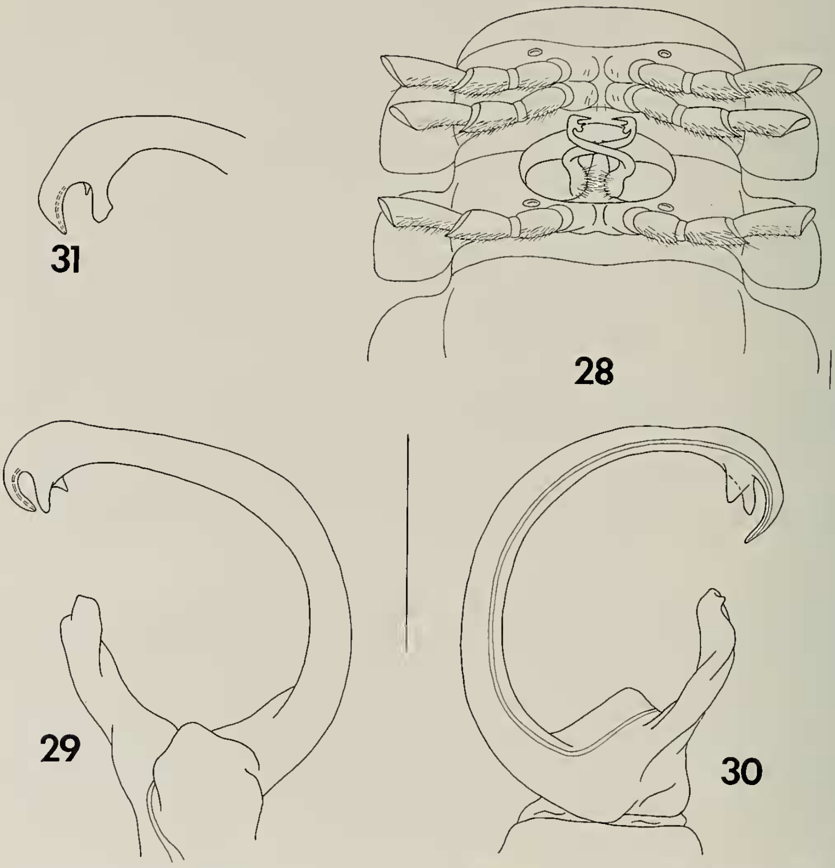
Distribution. — The Watauga River appears to form the southern boundary for this form, which ranges northward into the Ridge and Valley Province to the northern part of southwestern Virginia. It is the only species of *Dixioria* occurring in all three states. Material was examined as follows:

VIRGINIA. — *Tazewell Co.,* Burkes Garden, spring on NE slope of Beartown Mtn., M, 28 August 1977, R.L. Hoffman (RLH). *Bland Co.,* 10 mi. SW Bland, along US hwy. 52 near summit of Big Walker Mtn., 2M, F, 24 June 1950, R.L. Hoffman and J.A. Fowler (NMNH). *Wythe Co.,* Big Walker Mtn., M, 5 May 1955, collector unknown (RLH). *Grayson Co.,* Mt. Rogers, 2M, F, 1 July 1947, R.L. Hoffman and H.I. Kleinpeter (NMNH) and 2M, 24 August

1978, D.W. Ogle (RLH) TYPE LOCALITY; and Comer's Rock Rec. area, 2M, F, 15 June 1950, L. Hubricht (RLH). *Washington Co.,* 4 mi. SW Konnarock, base of Laurel Mtn., 2M, F, 28 April 1951, L. Hubricht (RLH).

TENNESSEE. — *Johnson Co.,* Backbone Rock Rec. Area., Cherokee Nat. For., approx. 4 mi. S Damascus, VA, 2M, F, 11 July 1962, and M, 2 June 1974, R.L. Hoffman (RLH); and along US hwy. 421, 1 mi. W NC state line, several MM, FF, 1 May 1965, collector unknown (RLH).

NORTH CAROLINA. — *Ashe Co.,* 14 mi. NW Jefferson, along co. rd. 1359, 0.5 mi. S. jct. co. rd. 1360, 4M, 3F, 17 June 1980 (NCSM A3295); 12 mi. NW Jefferson, along co. rd. 1356, 0.8 mi. SE jct. co. rd. 1358, 4M, 17 June 1980 (NCSM A3297); 10 mi. NW Jefferson, along co. rd. 1319, 1.7 mi. S jct. co. rd. 1320, M, 21 July 1972 (NCSM 1180); 8.5 mi. SW Jef-



Figs. 28-31. *Sigmoria (Dixioria) coronata.* 28, gonopods *in situ,* ventral view of paratype. 29, telopodite of left gonopod of holotype, medial view. 30, the same, lateral view. 31, peak and distal zone of male from Bland Co., VA, medial view. Scale line for fig. 28 = 1.00 mm; line for other figs. = 1.00 mm for each.

ferson, along co. rd. 1100 at Long Hope Cr., 3M, 2F, 17 June 1980 (NCSM A3299); Bina, several MM, FF, 17 May 1964, R.L. Hoffman (RLH); and between Idlewood and Gap Cr., 2M, F, 1 May 1965, collector unknown (RLH). *Watauga Co.*, 3 mi. SE Zionville, headwaters of Meat Camp Cr., M, 3F, 5 September 1971, R.L. Hoffman and L.S. Knight (RLH); 8 mi. NW Boone, along co. rd. 1213, 1.4 mi. SE jct. co. rd. 1201, 4M, 3F, 19 June 1980 (NCSM A3308); and 4 mi. N Vilas, along US hwy. 421, M, 11 June 1962, R.L. Hoffman (RLH).

Remarks. — As shown in figures 29 and 31, the types of *pela fowleri* closely resemble those of *coronata.* The slightly wider gap between the tooth and distal zone could result from a slightly different orientation of the structure for drawing. This is clearly insignificant and *p. fowleri* is placed in synonymy under *coronata,* making it the northernmost representative of *Dixioria.* It occurs sympatrically and perhaps syntopically with *brooksi* at Backbone Rock Recreation Area, Johnson County, Tennessee.

Sigmoria (Dixioria) wrighti (Hoffman), new combination, new status

Figs. 32-34

Dixioria pela wrighti Hoffman, 1956a:15, Fig. 1f.

Type specimens. — Male holotype (NMNH) collected by R.L. Hoffman, 3 August 1949, from Avery Co., NC, approximately 5 mi NE Linville, on the east side of Grandfather Mountain. The female allotype and male paratype, which Hoffman (1956a) reported to be in the NMNH, were not examined.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, curved caudad apically; acropodite thin and fragile, configuration a variably continuous curve directed downward to or below level of prefemoral process, forming complete or nearly complete circle; anterior bend broad, poorly defined; peak variably rounded, apex near midlength; apical curve broad, poorly defined, distal zone long, not coplanar with basal zone, curving broadly dorsad and more abruptly into arch distal to midlength; tooth present near midlength of distal zone, relatively long and nearly overlapping level of tip of acropodite, configuration variably quadriform with sides and distal margin irregular to serrate; accessory tooth arising at level of tooth, triangular to spiniform; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae.

Gonopods *in situ* (Fig. 32, not this specimen) with acropodites projecting mediad and crossing each other near midlengths in midline, curving broadly over opposite sides of aperture then back toward midline with tips overlapping, curvatures located entirely within aperture. Gonopod structure as follows (Fig. 33-34): prefemoral process relatively long, moderately thick, bent caudad apically, tip subacuminate, directed toward anterior bend. Acropodite relatively thin and fragile, configuration a smoothly continuous curve overhanging and extending well beyond level of prefemoral process, curving downward to or below level of latter forming nearly complete circle; basal zone relatively short, broadly curved; anterior bend broad, poorly defined; peak gently rounded, apex in midlength, sides not expanded; apical curve broad, poorly defined; distal zone moderately long, curving broadly into arch and extending beyond level of tooth, not coplanar with basal zone; tip subacuminate, directed toward anterior bend. Medial and lateral flanges absent. Tooth located near midlength of distal zone, relatively long, sides parallel, with four apical dentations; accessory tooth arising from inner surface of distal zone at same location, shorter and apically acute; partly obscured in medial view. Prostatic groove crossing to lateral side on prefemur, continuing to terminal opening.

Variation. — The degree of jaggedness or serration of the tooth varies on each individual, and there may be from three to five marginal dentations. The acropodite arch is also flattened more in some males, but the distal zone always extends to near the level of the prefemoral process.

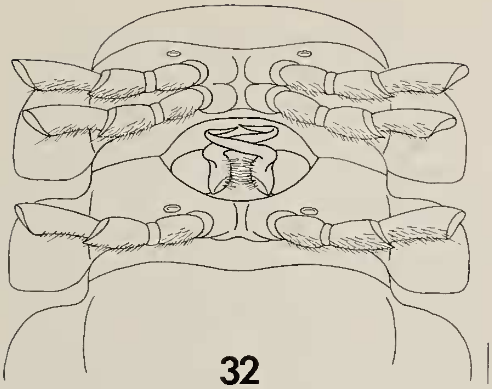
Ecology. — *Sigmoria (D.) wrighti* is a cove dwelling species.

Distribution. — A narrow area in the Blue Ridge Province between the Linville and Watauga rivers, extending onto the escarpment in Caldwell County, North Carolina. Specimens were examined as follows:

TENNESSEE. — *Johnson Co.,* along US hwy. 321, 1 mi. W NC state line, 2M, 3F, 1 May 1965, collector unknown (RLH).

NORTH CAROLINA. — *Watauga Co.,* 2 mi. W Sugar Grove, along US hwy. 321, M, 1 May 1965, collector unknown (RLH); 9 mi. W Boone, along co. rd. 1157, 0.1 mi. S jct. co. rd. 1123, 4M, F, 19 June 1980 (NCSM A3314); 7 mi. SW Boone, along NC hwy. 105, 0.8 mi. SW jct. co. rd. 1559, 2M, 19 June 1980 (NCSM A3315); and along US hwy 221 near Caldwell Co. line, M, 31 July 1931, A.W. Petrunkevitch (PMNH). *Avery Co.,* 4.1 mi. S Elk Park, along NC hwy. 194, 3M, 3F, 20 May 1956, R.L. Hoffman (RLH); between Linville and Banner Elk, M, 15 June 1953, R.L. Hoffman (RLH); 13.5 mi. N Newland, jct. US hwy. 321 and co. rd. 1316, M, 19 June 1980 (NCSM A3310); 7 mi. E Newland, along co. rd. 1514, 1 mi. E jct. US hwy. 221, 2M, 20 June 1980 (NCSM A3316); 8 mi. SW Newland, along co. rd. 1530, 0.4 mi. N jct. co. rd. 1511, M, F, 20 June 1980 (NCSM A3318); and 5 mi. NE Linville, along US hwy. 221 on E side Grandfather Mtn., M, 3 August 1949, R.L. Hoffman (NMNH); TYPE LOCALITY. *Caldwell Co.,* Edgemont, 2M, F, 22 June 1980 (NCSM A3333).

Figs. 32-36. 32-34, *Sigmoria (Dixioria) wrighti.* 32, gonopods *in situ,* ventral view of male from Watauga Co., NC. 33, telopodite of left gonopod of holotype, medial view. 34, the same, lateral view. 35-36, *Sigmoria (Dixioria) watauga,* holotype. 35, telopodite of left gonopod, medial view. 36, the same, lateral view. Scale line for fig. 32 = 1.00 mm; line for other figs. = 1.00 mm for each.



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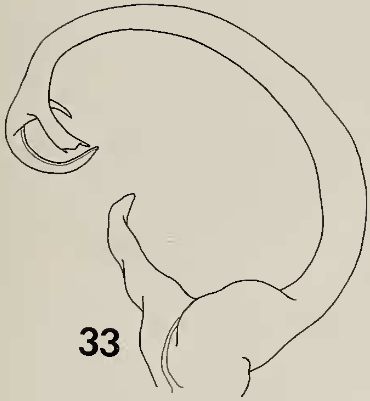

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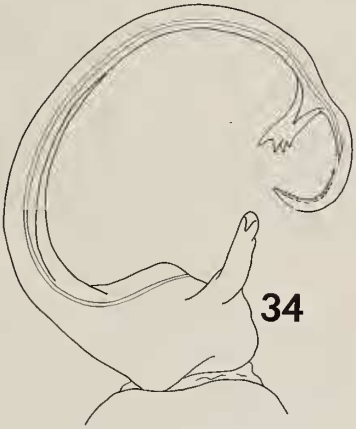

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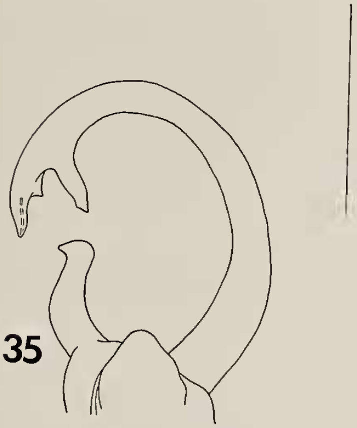

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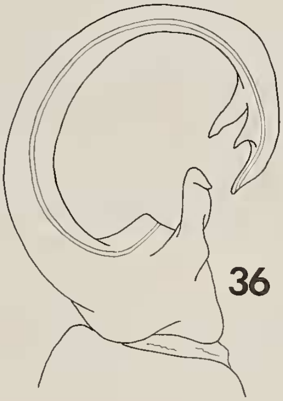

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Sigmoria (Dixioria) watauga Shelley, new species Figs 35-36

Type specimens. — Male holotype (NCSM 2008) and five male and seven female paratypes collected by R.M. Shelley, 8 September 1973, from yard of residence on Goforth Rd., 0.5 mi. N US highway 321, Blowing Rock, Watauga Co., NC. Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process relatively long, bisinuately curved; acropodite moderately thick and heavy, configuration a smooth continuous curve extending slightly beyond level of prefemoral process and directed downward toward latter; anterior bend and apical curve broad, poorly defined; peak gently curved, apex at midlength; distal zone moderately long, not coplanar with basal zone, directed downward toward prefemoral process; tooth present near midlength of distal zone, relatively long, apically subacuminate and irregular; accessory tooth short and triangular, arising distal to latter and fully visible in medial view; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots, collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Length 38.2 mm, maximum width 8.0 mm, W/L ratio 20.9%, depth/width ratio 67.5%. Segmental widths as follows:

collum 6.8 mm	15th 7.6
2nd 7.2	16th 6.8
3rd 7.8	17th 6.0
4th-14th 8.0	18th 5.0

Somatic features as in *l. latior,* with following exceptions:

Width across genal apices 3.9 mm, interantennal isthmus 1.6 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres $2>3>4>5=6>1>7$. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 10-10, labral about 16-16.

Dorsum smooth, polished, becoming slightly coriaceous on anterior halves of paranota. Collum broad, ends extending well below those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 12, blunt on segments 13-16. Peritremata distinct, strongly elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with moderate process between 3rd legs, length equal to widths of adjacent coxae; 5th sternum with two low, rounded, medially coalesced knobs between 4th legs and more separated, equivalent projections between 5th legs; 6th sternum convexly recessed between 7th legs to accommodate apical curves of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna generally flat, with variably broad, shallow, central impressions. Coxae with low, rounded tubercles beginning on segment 16; prefemoral spines beginning on segment 6, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 3.9 mm wide and 1.4 mm long at midpoint, without indentations, sides elevated above metazonal surface. Gonopods *in situ* with acropodites projecting mediad and crossing in midline, curving broadly over opposite side of aperture and extending dorsad, lying entirely over aperture. Gonopod structure as follows (Figs. 35-36): prefemoral process relatively long, bisinuate, apically subacuminate. Acropodite moderately thick and heavy, configuraton a smooth, continuous curve extending slightly beyond level of prefemoral process and curving downward in medial view (dorsad); basal zone moderately long, gently curved; anterior bend broad, poorly defined, continuous through peak with apical curve; peak relatively short, gently curved, apex at midlength; apical curve broad, poorly defined; distal zone moderately long, curving slightly laterad from peak and not coplanar with basal zone, projecting downward in medial and lateral views and extending to level of prefemoral process; tip subacuminate, directed toward coxa. Medial and lateral flanges absent. Tooth moderately long, apically subacuminate and irregular, located near midlength of distal zone; accessory tooth short and acute, arising distal to tooth and fully visible in medial view. Prostatic groove crossing to lateral side on prefemur and continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 39.4 mm, maximum width 8.4 mm, W/L ratio 21.3%, depth/width ratio 69.0%. Cyphopods *in situ* with openings of valves and corners of receptacles visible in aperture. Receptacle moderate, cupped around lateral sides of valves, surface rugulose. Valves small, equal, surfaces finely granulate.

Variation. — The gonopods are all quite similar. The tooth is slightly longer in western populations, and the midlength bend of the prefemoral process is considerably broader in that from Wilkes County.

Ecology. — *Sigmoria (D.) watauga* is primarily a cove species, although it can occur away from water sources. The type specimens were found under ivy, in moist litter, in corners of walkways, and in the basement of the residence at Blowing Rock.

Distribution. — A triangular area in the Blue Ridge Province of North Carolina, mostly in Watauga County. The species is common in the communities of Boone and Blowing Rock. Specimens were examined as follows:

NORTH CAROLINA. — *Watauga Co.,* 12 mi, WNW Boone, along US hwy. 321, 1.5 mi. N Avery Co. line, 2M, 129 June 1980 (NCSM A3309); Boone, Appalachian State Univ. campus, 2M, 3F, 26 April 1974 (NCSM 2212); 1.9 mi. S Boone, along co. rd. 1549, 0.7 mi. jct. co. rd. 1550, 4M, 26 April 1984 (NCSM 2216); 6.2 mi. E Boone, along co. rd. 1508, 1.2 mi. S jct. Blue Ridge Pkwy., 4M, 3F, 18 June 1980 (NCSM A3303); 2.2 mi. N Blowing Rock, along co. rd. 1541, 1.5 mi. N jct. co. rd. 1552, 2M, 26 April 1974 (NCSM 2221); and Blowing Rock, residence on Goforth Rd., 0.5 mi. N jct. US hwy. 321, 6M, 7F, 8 September 1973 (NCSM 2008) TYPE LOCALITY. *Wilkes Co.,* 18.1 mi. WNW Wilkesboro, Jeffress Pk. Recreation area on Blue Ridge Pkwy., 4M, 2F, 18 June 1980 (NCSM A3302).

Remarks. — The male from Boone that Hoffman (1956a) considered an intergrade between *pela wrighti* and *p. coronata* is referable to *watauga.*

Sigmoria (Dixioria) brooksi (Hoffman), new combination Figs. 37-40

Dixioria pela brooksi Hoffman, 1956a:12, Fig. 1d.
Dixioria brooksi Hoffman, 1969:227.

Type specimens. — Male holotype and male paratype (NMNH) collected by Dr. and Mrs. S.T. Brooks, 14 August 1941, on Holston Mountain near Damascus, Washington Co., VA. Hoffman (1956a) stated that male and female topoparatypes were deposited in the Carnegie Museum, Pittsburgh, PA, but I did not find them in a visit there in 1978.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, thick, and linear, tapering distad to acuminate tip; acropodite moderately thick and heavy, configuration an upright, open arch with apex overhanging level of prefemoral process; anterior bend sharp, well defined; peak moderately long and straight, outer margin expanded distad into broadly rounded lobe forming apex of arch; distal zone short, terminating well above prefemoral process, directed laterad from peak and not coplanar with basal zone, sides tapering to acuminate tip directed toward basal zone; medial and lateral flanges absent; tooth present on distal extremity of peak, short and truncate, extending to same level as tip of distal zone, distal margin linear, angling to lower inner corner; accessory tooth present, short and acute, arising from base of tooth, obscured by latter in medial view.

Color in Life. — Unknown. Hoffman (1956a) did not report this, and there is no fresh material. However, faded markings on the preserved specimens indicate the coloration of other members of *Dixioria.*

Holotype. — Length 35.2 mm, maximum width 7.6 mm, W/L ratio 21.6%, depth/width ratio 60.5%. Segmental widths as follows:

collum	5.4 mm	13th-15th	7.0
2nd	6.9	16th	6.8
3rd	7.2	17th	6.1
4th-12th	7.6	18th	4.9

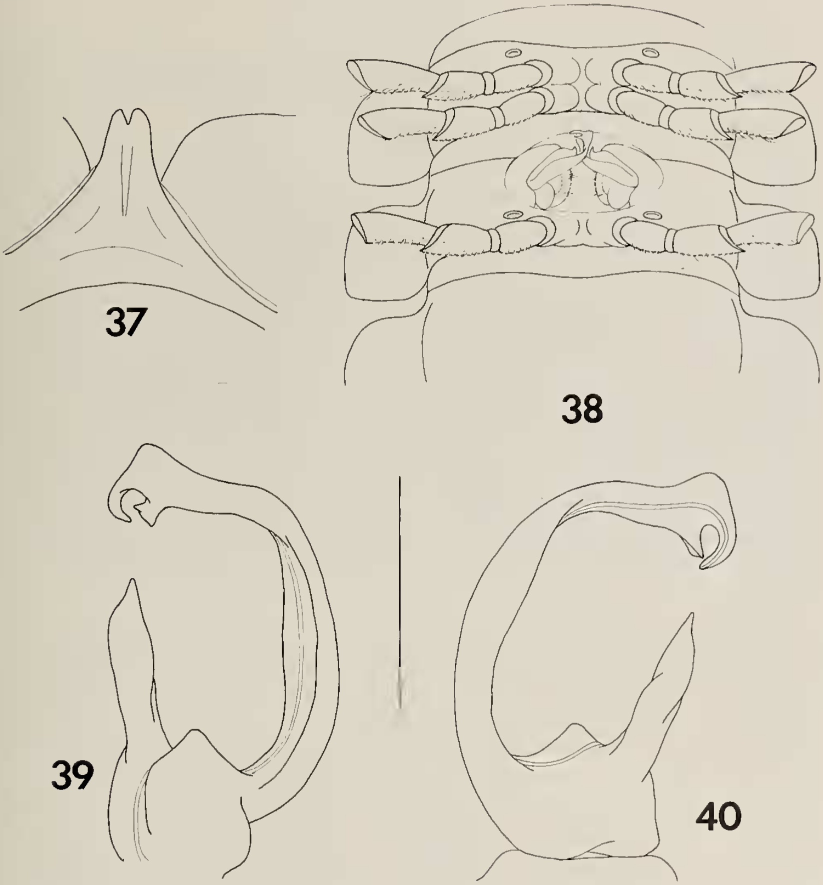
Somatic features similar to those of *I. latior,* with following exceptions:

Width across genal apices 3.9 mm, interantennal isthmus 1.4 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres $2 > 3 > 4 = 5 = 6 > 1 > 7$. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 12-12, labral about 18-18.

Dorsum smooth, polished, slightly coriaceous on anterior halves of paranota. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 13, blunt on 13-15, acute on remaining segments. Peritremata moderately distinct, slightly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with moderate process between 3rd legs, length equal to widths of adjacent coxae (Figs. 37); that of segment 5 with slight medial process between 4th legs, much shorter than widths of adjacent coxae, and low, rounded, elevated areas between 5th legs; that of segment 6 with moderate, convex recession between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on segments 8-10, flattened and plate-like thereafter. Coxae with low, blunt tubercles arising on segment 13; prefemoral spines arising on segment 8, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 3.2 mm wide and 1.9 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 38, not this specimen) with acropodites angling mediad and apices lying over and under each other in midline, extending forward slightly beyond anterior margin. Gonopod structure as follows (Figs. 39-40): prefemoral process relatively long, linear, tapering distad to acuminate tip, directed toward distal zone. Acropodite moderately thick and heavy, well sclerotized, arch upright, bent abruptly at 2/3 length and extending to but not beyond level of prefemoral



Figs. 37-40. *Sigmoria (Dixioria) brooksi.* 37, process of 4th sternum of holotype, caudal view. 38, gonopods *in situ,* ventral view of male from Johnson Co., TN. 39, telopodite of left gonopod of holotype, medial view. 40, the same, lateral view. Scale line for fig. 38 = 1.00 mm; line for other figs. = 1.00 mm for 37, 1.23 mm for 39-40.

process; basal zone relatively long, nearly straight; anterior bend sharp, well defined; peak moderately long and linear, outer margin expanded distad into rounded lobe forming highest point on acropodite arch; apical curve sharp, well defined; distal zone short, angling slightly laterad from peak, not coplanar with basal zone, directed downward toward prefemur then bending into arch, nearly overlapping tooth; tip subacuminate, directed toward basal zone. Medial and lateral flanges absent. Tooth short, apically broad and truncate, outer corner slightly produced, located at distal extremity of peak; accessory tooth equal in length to, and arising from base of, tooth, obscured in medial view, apically acuminate. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Male Paratype. — The male paratype agrees with the holotype in all particulars.

Female Paratype. — As the specimen supposedly at the Carnegie Museum could not be located, the female characters of *brooksi* are unknown.

Variation. — The male from Tennessee agrees closely with the holotype.

Distribution. — Known from the type locality and the following site, which is only about four miles southeast.

Remarks. — Although *brooksi* possesses an accessory tooth and resembles *coronata* in the general form of the acropodite and the short distal zone that curves inward, nearly overlapping the tooth, it is not conspecific. The two occur sympatrically at Backbone Rock Recreation Area and hence are reproductively isolated. The male of *brooksi* was even discovered in a vial with one of *coronata,* suggesting that they are syntopic. The course of the prostatic groove differs, as it crosses to the lateral surface at the anterior bend in *brooksi* and on the prefemur in *coronata.* Likewise, they are distinguished by the configuration of the peak, which is expanded into a distolateral lobe in *brooksi* and is nearly linear in *coronata.* The lobe in *brooksi* culminates the tendency toward enlargement at this position found in *dactylifera* and *acuminata.* It is similar in appearance to, and apparently convergent with, that of *translineata (Falloria)* (compare Figs. 39-40 with Figs. 68-69 in Shelley (1981a)).

TENNESSEE. — *Johnson Co.,* Backbone Rock Recreation Area, Cherokee National Forest, along TN hwy. 41 about 4 mi. S of Damascus, VA and the state line, M, 2 June 1974, R.L. Hoffman and L.S. Knight (RLH).

Remarks. — Although *brooksi* possesses an accessory tooth and resembles *coronata* in the general form of the acropodite and the short distal zone that curves inward, nearly overlapping the tooth, it is not conspecific. The two occur sympatrically at Backbone Rock Recreation Area and hence are reproductively isolated. The male of *brooksi* was even discovered in a vial with one of *coronata,* suggesting that they are syntopic. The course of the prostatic groove differs, as it crosses to the lateral surface at the anterior bend in *brooksi* and on the prefemur in *coronata.* Likewise, they are distinguished by the configuration of the peak, which is expanded into a distolateral lobe in *brooksi* and is nearly linear in *coronata.* The lobe

in *brooksi* culminates the tendency toward enlargement at this position found in *dactylifera* and *acuminata*. It is similar in appearance to, and apparently convergent with, that of *translineata (Falloria)* (compare Figs. 39-40 with Figs. 68-69 in Shelley (1981a)).

Sigmoria (Dixioria) dactylifera (Hoffman), new combination Figs. 41-44

Dixioria dactylifera Hoffman, 1956a:15-16,Fig. 2.

Type specimens. — Male and female paratypes (AMNH, NMNH) collected by C.M. and R.D. Breeder, 22 August 1910, at Mill Hill (precise location unknown), Ashe Co., NC. The male holotype said by Hoffman (1956a) to be deposited in the AMNH is not there and apparently is lost.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process moderately long and gently curved ventrad, apically subacuminate; acropodite moderately thick and heavy, configuration an open arch leaning over and extending slightly beyond level of prefemoral process; anterior bend broad, poorly defined; peak relatively long, margins essentially straight; apical curve sharp, well defined; distal zone short, terminating well above level of prefemoral process, directed laterad from peak and not coplanar with basal zone, sides tapering to acuminate tip directed parallel to prefemoral process; medial and lateral flanges absent; tooth present on distal extremity of peak, relatively long, extending below level of distal zone, sides parallel, distal margin linear, inner apical corner produced to form subacuminate tip projecting inward into arch and directed toward basal zone; accessory tooth absent.

Color in Life. — Paranota bright lemon yellow; metaterga dark glossy black without stripes or spots; collum with narrow yellow stripe along anterior margin connecting paranotal markings.

Male Paratype. — Length 56.9 mm, maximum width 7.4 mm, W/L ratio 20.1%, depth/width ratio 60.8%. Segmental widths as follows:

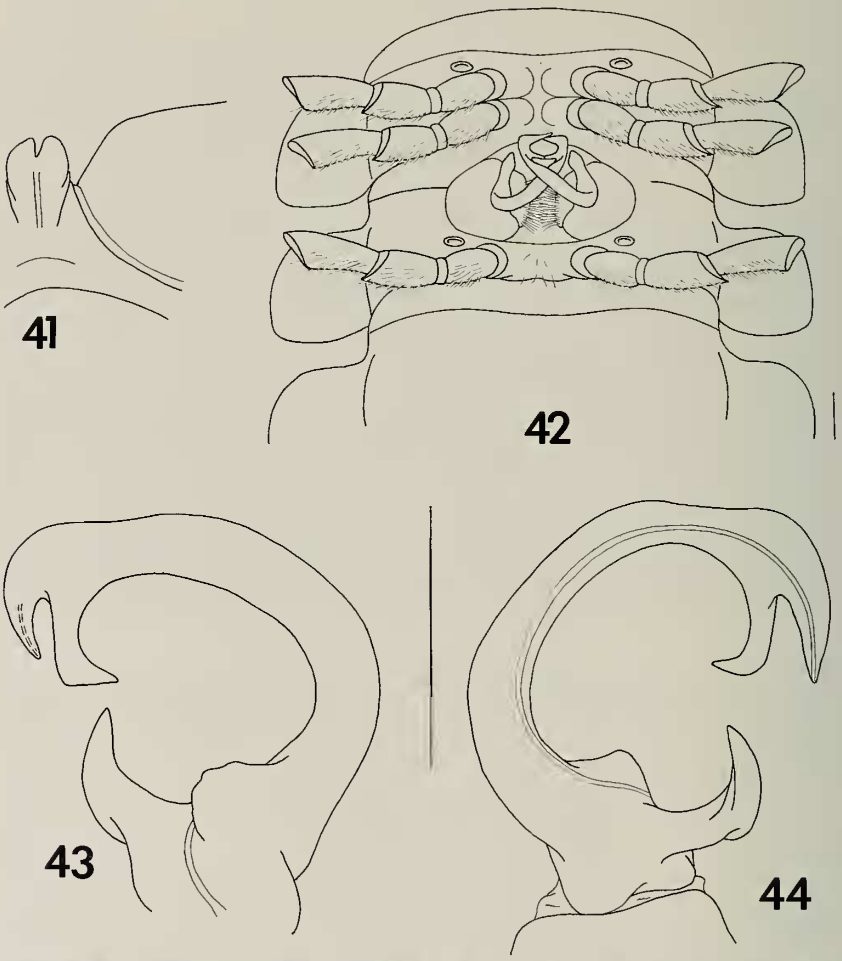
collum 5.9 mm	15th 7.2
2nd 6.5	16th 6.8
3rd 7.0	17th 5.8
4th-14th 7.4	18th 4.2

Somatic features similar to those of *l. latior*, with following exceptions:

Width across genal apices 3.9 mm, interantennal isthmus 1.7 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2> 3> 5> 6> 4> 1> 7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 9-9, labral about 12-12, merging with clypeal series and continuing for short distance along genal borders, about 3 setae per side.

Dorsum smooth, polished, slightly coriaceous on anterior halves of paranota and extending mediad along margins of strictures. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 13, blunt on 14-16, acute on remaining segments. Peritremata moderately thick and distinct, well elevated above paranotal surfaces, ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with small process between 3rd legs, shorter than widths of adjacent coxae (Fig. 41); that of segment 5 with low projection between 4th legs, much shorter than



Figs. 41-44. *Sigmoria (Dixioria) dactylifera.* 41, process of 4th sternum of paratype, caudal view. 42, gonopods *in situ,* ventral view of male from Mt. Jefferson St. Pk., Ashe Co., NC. 43, telopodite of left gonopod of paratype, medial view. 44, the same, lateral view. Scale line for fig. 42 = 1.00 mm; line for other figs. = 1.00 mm for each.

widths of adjacent coxae, and higher, flattened, elevated areas between 5th legs; that of segment 6 with deep, convex depression between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on segments 8-11, with variably broad, shallow, central depressions on remaining segments. Coxae with low blunt tubercles arising on caudal legs of segment 13; prefemoral spines arising on segment 6, becoming longer and sharper caudally.

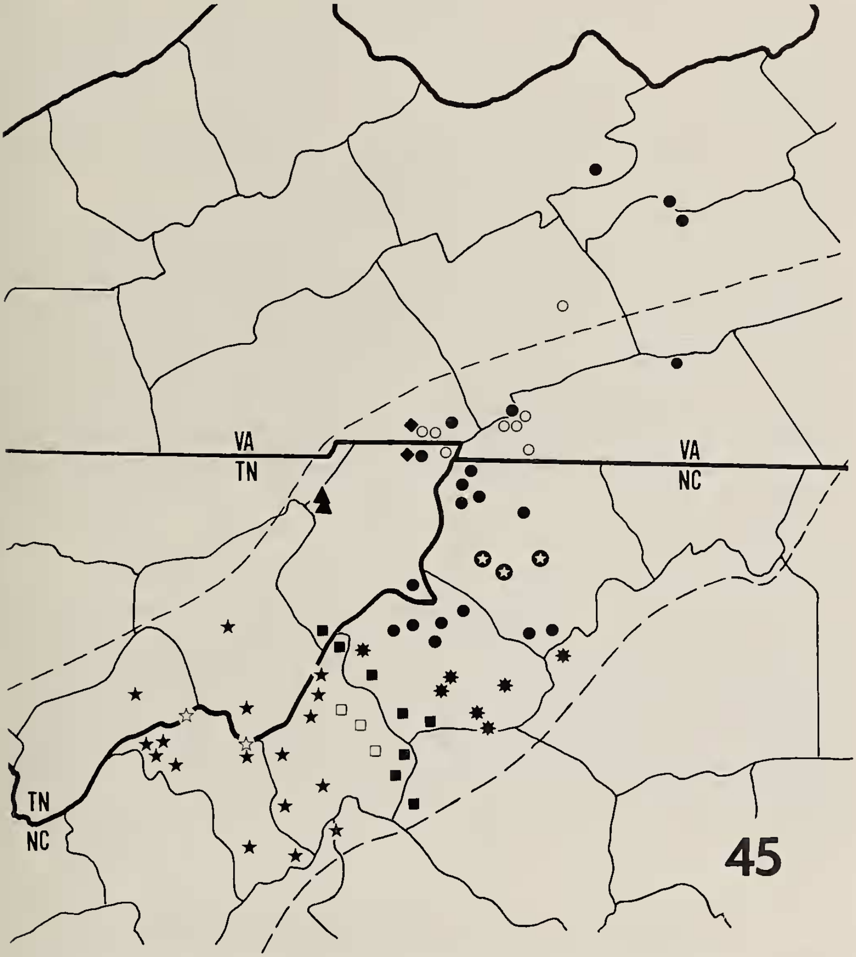


FIG. 45. Distribution of the subgenus *Dixioria* in North Carolina, Tennessee, and Virginia. Stars, *pela;* triangles, *acuminata;* dots, *coronata;* squares, *wrighti;* asterisks, *watauga;* diamonds, *brooksi,* stars in dots, *dactylifera.* Open symbols represent unconfirmed records from Hoffman (1956a) that are believed to be correct. The dashed lines show the approximate boundaries of the Blue Ridge Province.

Gonopodal aperture ovoid, 3.3 mm wide and 1.8 mm long at midpoint, indented slightly aneriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 42, not this specimen) with acropodites crossing in midline of aperture, curving slightly over opposite side then back toward midline with apices overlapping, extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 43-44): Prefemoral process moderately long, thick, and heavy, curving broadly ventrad and directed toward tooth, tip subacuminate. Acropodite moderately thick and heavy, arch broadly curved, leaning over and extending slightly beyond level of prefemoral process; basal zone short, broadly curved; anterior bend broad, poorly defined; peak relatively long and straight, apex near midlength; apical curve sharp, well defined; distal zone short, curving strongly laterad from peak and not coplanar with basal zone, directed downward from peak in medial view with only very slight curve; tip acuminate, directed parallel to prefemoral process. Medial and lateral flanges absent. Tooth long, extending below level of distal zone, directed linearly from distal extremity of peak with sides parallel, inner apical corner produced to form acuminate tip projecting inward into arch and directed toward basal zone; accessory tooth absent. Prostatic groove crossing to lateral side on prefemur, continuing on this surface to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype.

Female Paratype. — Length 37.2 mm, maximum width 7.9 mm, W/L ratio 21.2%, depth/width ratio 64.6%. Cyphopods *in situ* with receptacle visible in aperture, valves directed laterad. Receptacle large, hood-like, enveloping medial and ventral surfaces of valves, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — All males of *dactylifera* are nearly identical to each other.

Ecology. — The male I collected in Mt. Jefferson State Park was discovered at the picnic area near the summit under moist litter in a deciduous forest. The site lacked rhododendron and a water source, and could not be classified as a cove.

Distribution. — Known only from three localities in the northwestern corner of North Carolina. Material was examined as follows:

NORTH CAROLINA. — *Ashe Co.,* Mill Hill, exact location unknown, 6M, 5F, 22 August 1910, C.M. and R.D. Breeder (AMNH, NMNH) TYPE LOCALITY; 2 mi. SE Creston, Three-Top Mtn., 4M, 4F, 23 July 1963, R.L. Hoffman (RLH); and Mt. Jefferson St. Pk., M, 29 August 1976 (NCSM A1412).

Remarks. — The principle diagnostic features of *dactylifera* are the distinctive configuration of the tooth and the absence of the accessory tooth.

SIGMORIA (SIGMORIA) Chamberlin, new status

Sigmoria Chamberlin, 1939:7. Hoffman, 1950:1-2; 1979:158. Chamberlin and Hoffman, 1958:49. Jeekel, 1971:287. Shelley, 1981a:16-18.

Type species. — *Sigmoria munda* Chamberlin, 1939, by original designation.

Diagnosis. — Paranota yellow to red, metatergal color pattern variable, either uniformly black or with concolorous stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture and inserting between 7th legs; acropodites moderately thick, oriented normally on coxa with inner surface directed anteriomediad; basal zone without modifications; with variable laminate medial flange located on peak; with or without variable lateral flange and variable tooth on peak distal to flange; tip either reflexed or with this configuration.

Remarks. — The nominate subgenus occupies a broad area from southern West Virginia to the Savannah River and the Atlantic Ocean. In the north it overlaps all of *Dixioria* and the southern extremity of *Rudiloria,* and in the south it overlaps the South Carolina forms of *Cleptoria* and all species of *Croatania* except *yemassee.* Although less common in the mountains, it ranges westward into the central Blue Ridge Province and overlaps parts of *Sigiria* and *Cheiropus.* Most of its range is due to the widespread, ubiquitous *latior,* a clinally continuous species composed of three geographic races connected through a broad area of intergrades (Shelley 1976, 1981a). In the western Piedmont of North Carolina occurs a second species, *stenoloba,* that apparently arose from *latior* by ecological isolation and is comprised of two allopatric populations. Two additional, localized species occur in the eastern Piedmont and Fall Zone of southern South Carolina. They are sufficiently different from *latior* and *stenoloba* that I divide *Sigmoria s. str.* into two species groups.

The *Latior* Group

In the *latior* group, the acropodites are moderately thick and heavy, the anterior bend and apical curve are sharp and well defined, and the peak is flattened and constitutes about 1/3 of the total length. The medial flange is variably broad, located on the proximal part of the peak, and clearly demarcated from the acropodite stem. The distal zone terminates in a reflexed tip; has a long, narrow flange; and usually exhibits a tooth distal to the medial flange. The *latior* group overlaps partly the *quadrata* group, and its range is essentially that of the subgenus.

Components. — *latior* (Brolemann) [*l. latior, l. munda* Chamberlin, *l. hoffmani* Shelley], *stenoloba* Shelley.

Additional Records. — *l. latior* — VA, Patrick Co., Blue Ridge Parkway at mile 174.3, M, 23 June 1984, R.L., and C. Hoffman (RLH); *l. munda* — SC, Spartanburg Co., Spartanburg, M, 3 October 1943, R.L. Wenzel (FMNH).

The *Quadrata* Group

The acropodites in this group are characterized by reduced medial flanges and simple tips that project inward into the arches at distinct angles from the distal zones. A lateral flange may or may not be present, but other acropodal specializations are absent. The prefemoral process is moderately long. The two species occupy small areas in the eastern Piedmont and Fall Zone of southern South Carolina.

Components. — *quadrata* Shelley, *laticurvosa* Shelley.

Additional Record. — *quadrata* — SC, Lexington Co., Leesville, M, 7 October 1949, L. Brodie (FMNH).

SIGMORIA (CROATANIA) Shelley, new status

Croatania Shelley, 1977:305-306. Hoffman, 1979:159.

Type species. — *Croatania catawba* Shelley, 1977, by original designation.

Diagnosis. — Paranota yellow or red, metaterga either uniformly black or with concolorous stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture, inserting between 7th legs; prefemoral process very large, usually extending beyond level of tip of distal zone; acropodites moderately thick and heavy to massive, well sclerotized, oriented normally on coxa with inner surface directed anteriomediad; basal zone with proximomedial edge expanded and irregularly notched, basalmost projection largest, spiniform; medial flange variable but laminate, located entirely on peak, expanded distad into lobe, latter sometimes detached from flange; lateral flange present, lobe-like, usually clearly demarcated from acropodite stem; tip blunt.

Remarks. — The subgenus *Croatania* occurs to the east and north of *Cleptoria* in piedmont South Carolina and ranges into south-central North Carolina. The center of diversity is the Broad River Valley of north-central South Carolina where *catawba, saluda,* and *simplex* are parapatric. The fourth species, *yemassee,* is allopatric in the outer Coastal Plain. The gonopods, widely separated and parallel *in situ* (see Fig. 46 of *simplex),* exhibit a number of specializations, the most obvious being an irregularly notched, proximomedial expansion of the basal zone, which varies in length and degree of jaggedness and is small and comparatively inconspicuous in *yemassee.* Three species — *catawba, saluda,* and *yemassee* — also have enormous prefemoral processes extending to or beyond the levels of the distal zones. Females of this group can be distinguished by the large, convoluted cyphopodal membrane, which protrudes through the medial corner of the aperture.

Croatania is composed of four species which are united in a single species group, the *catawba* group. They were illustrated and described in detail by Shelley (1977), and the gonopods are here redescribed in "sigmoid" terminology. New diagnoses and color descriptions are also presented along with new locality records for each species except *yemassee*. A discussion of variation is given for *simplex*.

Components. — *catawba* (Shelley), *saluda* (Shelley), *simplex* (Shelley), *yemassee* (Shelley).

Sigmoria (Croatania) catawba (Shelley), new combination

Croatania catawba Shelley, 1977:306-312, Figs. 1-2, 7, 11-12, 16. Filka and Shelley, 1980:28, Fig. 54.

The three new records of *catawba* add Cherokee County, South Carolina, to its known range and conform to the previous account of variation.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on peak and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process massive, globose basally, bent ventrad distal to midlength and narrowing to acuminate tip, extending beyond level of tip of acropodite; latter thick and heavy, arch high and rounded, extending to but not beyond level of prefemoral process; basal zone with ridge on inner surface, proximomedial edge expanded into deeply notched plate, basalmost projection in form of short spine; anterior bend poorly defined; peak moderately long, gently curved; apical curve well defined; distal zone short, angling into arch, tip blunt; medial flange arising at anterior bend, expanding distad into triangular lobe on distal extremity of peak; lateral flange in form of thick lobe on proximal part of distal zone, well demarcated from acropodite stem.

Color in Life. — Paranota bright lemon yellow, occasionally orange; metaterga black, without stripes; collum with or without broad concolorous stripe along anterior margin.

Holotype Gonopods. — Prefemur moderate with massive process arising on dorsal side, subglobose basally, widest proximal to midlength and blackened along inner edge, bent ventrad at 2/3 length and tapering to acuminate tip; latter directed toward anterior bend, extending well beyond level of distal zone. Acropodite thick and heavy, well sclerotized, arch upright, a smooth, continuous curve overhanging but not extending beyond level of prefemoral process; basal zone with ridge on inner surface, proximomedial edge expanded into deeply notched plate, basalmost projection enlarged into short spine; anterior bend broad, poorly defined; peak moderately long, gently curved, apex at midlength; apical curve sharp, well defined; distal zone short, coplanar with basal zone, angling into arch and directed toward latter; tip blunt. Medial flange arising proximad on peak, expanded distad into triangular lobe on distal extremity. Lateral flange in form of thick, heavily sclerotized lobe on proximal part of distal zone, well demarcated from latter. Prostatic groove running along lateral side of ridge on basal zone, crossing to lateral side of acropodite at anterior bend and continuing to terminal opening.

Distribution. — South-central piedmont North Carolina to north-central piedmont South Carolina (Shelley 1977). Specimens were examined from the following new localities:

SOUTH CAROLINA. — *Cherokee Co.,* 4.6 mi SE Blacksburg, along SC hwy. 5, 0.3 mi S jct. SC hwy. 68, F, 10 May 1977 (NCSM A1481). *Chester Co.,* 11.6 mi W Chester, Leeds Campground, Sumter Nat. For., 2M, F, 30 April 1977 (NCSM A1486); and 12.4 mi W Lowrys, along SC hwy. 9 at Broad R., 2M, 1 May 1977 (NCSM A1500). *Union Co.,* 0.1 mi N Jonesville, along SC hwy. 18, 2M, 2F, 2 May 1977 (NCSM A1505); 2.3 mi W Carlisle, along SC hwy. 24 at Cane Cr., 2M, 3F, 2 May 1977 (NCSM A1513); and 5.0 mi N Carlisle, along SC hwy. 86 at Neals Cr., Sumter Nat. For., 6M, 2F, 2 May 1977 (NCSM A1514).

Remarks. — The two males in sample A1500 from Chester County were found dead and lying on top of leaves. They had been recently decapitated by an unknown carnivore and were still pliable. One male lacked the head and collum, and the other had lost the head, collum, and segments 2 and 3. The bites were irregular and parts of the next segments had been destroyed, but there was no evidence of continuous chewing. The segments seem to have been removed by a single, clean bite, which stopped short of segment 5 and the anteriormost defensive glands. This situation is identical to that I reported for *Dicellarius t. talapoosa* (Chamberlin) from Cheaha Mountain, Alabama (Shelley 1984c).

Sigmoria (Croatania) saluda (Shelley), new combination

Croatania saluda Shelley, 1977:312-316, Figs. 3, 8, 13.

As with *catawba,* the new material of *saluda* conforms to previously known variation, but the range is expanded to encompass parts of Laurens, Lexington, Saluda, and Aiken counties, South Carolina. Its north-south distribution from the Enoree to the Savannah Rivers, is unchanged, but the area is extended eastward into the Fall Zone.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process large, sides parallel, curving broadly ventrad, apically bifurcate with medial component longer than lateral and extending beyond level of distal zone; acropodite thick and heavy, leaning dorsad and extending beyond level of prefemoral process; basal zone with proximomedial edge expanded into shallowly notched plate, basalmost projection enlarged into spine; anterior bend poorly defined; peak moderately long, gently curved; apical curve well defined; distal zone short, angling into arch, tip blunt; medial flange arising at anterior bend, expanding distad into triangular lobe on distal extremity of peak and proximal part of distal zone; lateral flange in form of thick lobe on proximal part of distal zone, well demarcated from latter.

Color in Life. — Paranota usually entirely red, color occasionally restricted to peritremata; metaterga black, without stripes; collum with red strip along anterior margin.

Holotype Gonopods. — Prefemoral process not globose basally, of nearly equal width throughout, broadly curved ventrad, bifurcate apically, medial component longer than lateral component and extending beyond level of distal zone, directed toward anterior bend. Acropodite thick and heavy, well sclerotized, arch broad, a smooth continuous curve leaning dorsad and extending well beyond level of prefemoral process; basal zone without ridge, proximomedial edge expanded into shallowly notched plate, longer and more irregularly notched than in *catawba,* basalmost projection enlarged into short spine. Anterior bend broad, poorly defined; peak moderately long, gently curved, apex at midlength; apical curve sharp, well defined; distal zone short, coplanar with basal zone, angling into arch and directed toward prefemur; tip blunt. Medial flange arising at anterior bend, expanding distad into broadly rounded lobe on distal extremity of peak and proximal part of distal zone. Lateral flange in form of thick, heavily sclerotized lobe on proximal part of distal zone, well demarcated from latter. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Distribution. — Central and south-central piedmont South Carolina between the Enoree and Savannah Rivers, ranging east into the Fall Zone. Specimens were examined from the following new localities:

SOUTH CAROLINA. — *Laurens Co.,* 11.2 mi NE Clinton, along SC hwy. 72 at Duncan Cr., M, F, 9 May 1977 (NCSM A1564); 8.6 mi. S Clinton, along SC hwy. 38 at Little R., 3M, 9 May 1977 (NCSM A1565); and 2.0 mi. NE Cross Hill, along SC hwy. 560 at Campbell Cr., M, 9 May 1977 (NCSM A1566). *Greenwood Co.,* 8.4 mi. SW Ninety Six, along SC hwy. 702, 0.2 mi. W Saluda Co. line, M, 4 May 1977 (NCSM A1524). *Newberry Co.,* 16.0 mi. NE Newberry, along SC hwy. 45 at Enoree R., M, F, 3 May 1977 (NCSM A1517); and 6.3 mi. E Newberry, along US hwy. 176 at Mud Cr., 4M, 2F, 3 May 1977 (NCSM A1521); 11.5 mi. E Newberry, along US hwy. 176, 0.1 mi. S Pomaria, 3M, 2F, 14 July 1979 (NCSM A2804); 6.5 mi. SE Newberry, along SC hwy. 244, 0.5 mi. E jct. SC hwy. 315, M, F, July 1979 (NCSM A2806); and 9.0 mi. SE Newberry, along SC hwy. 403 at Camping Cr., M, F, 14 July 1979 (NCSM A2805). *Richland Co.,* 20.0 mi. NW Columbia, along US hwy. 176 at Wateree Cr., F, 14 July 1979 (NCSM A2803); and 14.0 mi. NW Columbia, along SC hwy. 244 at Hollingshead Cr., 3M, F, 14 July 1979 (NCSM A2802). *Lexington Co.,* West Columbia, M, 3F, 24 June 1958, collector unknown (FSCA); 13.0 mi. W Lexington, along SC hwy. 59 at Little Cr., 3M, 15 July 1979 (NCSM A2813); and 5.2 mi. NE Leesville, along SC hwy. 158, 0.3 mi. S jct. SC hwy. 54, 3M, 23 November 1977 (NCSM A1809). *Saluda Co.,* 4.0 mi. WNW Batesburg, along US hwy. 178 at Clouds Cr., 2M, 23 November 1977 (NCSM A1807); 6.0 mi. S Saluda, along SC hwy. 193, 0.1 mi. W jct. SC hwy. 119, 5M, 3F, 15 July 1979 (NCSM A2811); and 6.5 mi. E Saluda, along US hwy. 178, 0.2 mi. W jct. SC hwy. 29, M, F, 15 July 1979 (NCSM A2811). *Edgefield Co.,* 1.9 mi. ENE Trenton, along SC hwy. 75 at Tiger Cr., 3M, 2F, 23 November 1977 (NCSM A1804); and 7.5 mi. S Edgefield, along SC hwy. 34 at Double Branch Cr., M, 16 July 1979 (NCSM A2821). *Aiken Co.,* Lexington Co. line on SC hwy. 109 at Chinquapin Cr., 2M, F, 15

July 1979 (NCSM A2818); and North Augusta, along SC hwy. 230, 1.7 mi. E I-20, 2M, 2F, 17 September 1980 (NCSM A3509).

Sigmoria (Croatania) simplex (Shelley), new combination Figs. 46-48

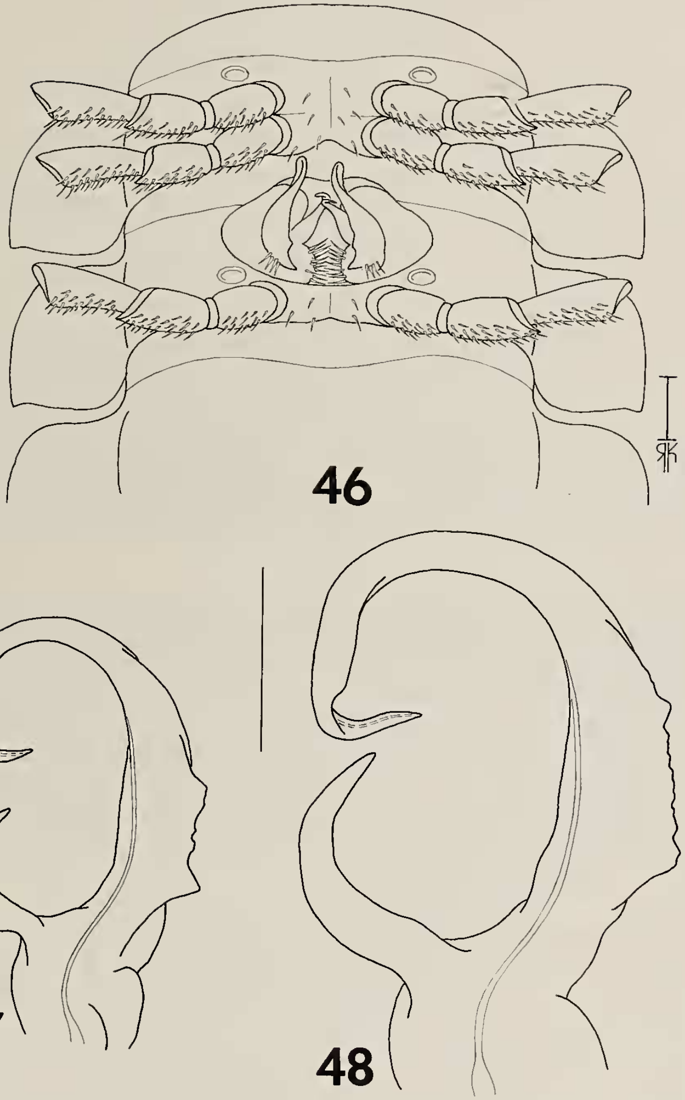
Croatania simplex Shelley, 1977:316-319, Figs. 4-5, 9, 14.

Priority for the name *simplex* is with this species, proposed four years before the one herein renamed *inornata (Sigiria).* The original description of *simplex* was based only on the type series from Chester County, South Carolina, and the range could not be reported, nor could variation be discussed aside from that demonstrated by paratypes.

Diagnosis. — A moderate-size species of *Sigmoria* with short medial flange located on distal extremity of peak or proximal part of distal zone and with yellow or red paranota, metaterga with or without narrow, concolorous transverse stripes; gonopods with following diagnostic characters: prefemoral process moderately long, curving broadly ventrad, apically acuminate or bifurcate; acropodite moderately thick, arch flattened or a smooth, continuous curve, overhanging and extending beyond level of prefemoral process; basal zone with proximomedial edge expanded into variably notched plate, basalmost projection largest; anterior bend poorly defined; peak moderately long, gently curved or flattened; apical curve variably defined; distal zone moderately long, curving broadly into arch or extending ventrad from peak and bent abruptly into arch at midlength, apically acuminate; medial flange represented by distal lobe and short preceding lamella, either located on distal extremity of peak or arising there and terminating near midlength of distal zone; lateral flange either absent or represented by widening in proximal portion of distal zone.

Color in Life. — Paranota bright lemon yellow, occasionally red; metaterga black, with or without concolorous stripes along caudal edges; collum with stripe along anterior margin.

Holotype Gonopods. — Prefemoral process moderately long (Fig. 47), terminating well below level of distal zone, crescent shaped, widest at 1/3 length, then tapering smoothly and continuously to acuminate tip, latter directed toward anterior bend. Acropodite moderately thick and heavy, arch upright, a smooth, continuous curve overhanging and extending beyond level of prefemoral process; basal zone without ridge, basal proximomedial expansion short, shallowly notched, basalmost projection enlarged into short spine; anterior bend broad, poorly defined; peak relatively short and high, gently rounded, apex at midlength; apical curve broad, poorly defined; distal zone moderately long, curving broadly into arch, tapering smoothly and continuously to acuminate tip; latter directed toward anterior bend. Medial flange short, inconspicuous, represented only by short, blunt tubercle and short attached lamella at level of apical curve, this homologous to lobe of *catawba.* Lateral flange indistinct, represented by broad rounded area at midlength of distal zone. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.



FIGS. 46-48. *Sigmoria (Croatania) simplex.* 46, gonopods *in situ,* ventral view of male from Fairfield Co., SC. 47, telopodite of left gonopod of holotype, medial view. 48, telopodite of left gonopod of male from Richland Co., SC. Scale line for fig. 76 = 1.00 mm; line for other figs. = 1.00 mm for 77; 0.64 mm for 48.

Variation. — Some specimens have yellow stripes along the caudal margins of the metaterga, whereas others, like the types, lack these markings. Both patterns were found 4.2 mi. N Columbia (samples A2800-2801), but there were no detectable anatomical differences. Material from Berkeley and Orangeburg counties had red paranota and stripes.

The gonopods of eastern populations vary considerably from the types, and a representative example is shown in Figure 48. Aside from occasional bifurcate individuals, as found in the type series, the prefemoral process is generally of the same shape throughout the range, although it becomes longer and narrower in eastern populations. In the Kershaw County males it projects beyond the level of the distal zone. The proximomedial expansion is shorter and less jagged in some males, and this does not conform to any geographic pattern. The medial flange, however, is broad and laminate in eastern forms, and the distal zone likewise projects inward into the arch of the acropodite at a sharper angle, often at right angles. The configuration shown in Figure 12 is actually more common and representative of *simplex* than that of the holotype, which is restricted to the northwestern range periphery and may represent a terminal population effect. Thus, the situation is similar to that in *macra (Cleptoria),* where the holotype is atypical for the species.

Distribution. — Farifield, Richland, Kershaw, Orangeburg, and Berkeley counties can be added to the distribution of *simplex,* which is now known from both the Piedmont and Coastal Plain of South Carolina. The type locality is the northernmost, as I have not found the species in Union, York or Lancaster counties. The range abuts that of *catawba* in Chester County, and in Richland County, *simplex* is segregated from *saluda* by the Broad River. Here and in Fairfield County the waterway is the western limit, but northern populations in Chester County do not extend to the river, being replaced on the eastern side by *catawba.* Material was examined from the following localities:

SOUTH CAROLINA. — *Chester Co.,* 7.2 mi. SE Chester, along SC hwy. 44, 0.7 mi. W jct. SC hwy. 347, F, 1 May 1977 (NCSM A1492); and 7.2 mi. SW Chester, along SC hwy. 42 at Sandy R., 4M, F, 1 May 1977 (NCSM A1502). *Farifield Co.,* 16.8 mi. NW Winnsboro, along SC hwy. 215, 0.5 mi. N jct. SC hwy. 302, 2M, 2F, 3 May 1977 (NCSM A1516); 12.0 mi NW Winnsboro, along SC hwy. 28 at Mobley Cr., 2M, 13 July 1979 (NCSM A2793); 7.0 mi. NW Winnsboro, along SC hwy. 303, 1.5 mi. N jct. SC hwy. 22, 2M, 2F, 13 July 1979 (NCSM A2792); 13.0 mi. SW Winnsboro, along SC hwy. 46 at Sawney's Cr., M, 2F, 13 July 1979 (NCSM A2788); 10.5 mi. SW Winnsboro, along SC hwy. 213 at Little R., 3M, 2F, 13 July 1979 (NCSM A2794); 9.5 mi. S Winnsboro, along SC hwy. 64 at Little Cedar Cr., 5M, F, 13 July 1979 (NCSM A2796); and 9.0 mi. NE Winnsboro, along SC hwy. 234 at Wateree Cr., M, 13 July 1979 (NCSM A2791). *Kershaw Co.,* 11.0 mi. NNW Camden, along SC hwy. 40 at Flat Rock Cr., 2M, F, 12 July 1979 (NCSM A2789). *Richland Co.,* 15.0 mi. NNE Columbia, along

SC hwy. 54 at Five Mile Cr., M, F, 13 July 1979 (NCSM A2798); 15.0 mi. NNW Columbia, along SC hwy. 967 at Horse Cr., 3M, F, 13 July 1979 (NCSM A2797); 12.0 mi. NNW Columbia, along SC hwy. 59, 0.1 mi. N jct. SC hwy. 215, M, 23 November 1977 (NCSM A1811); 7.0 mi. N Columbia, along SC hwy. 61 at North Branch Cr., 9M, 7F, 14 July 1979 (NCSM A2800-A2801); and 3.0 mi. N Columbia, along US hwy. 321 at Crane Cr., 2M, F, 14 July 1979 (NCSM A2799). *Orangeburg Co.*, Santee State Park, M, 9 September 1980 (NCSM A3494). *Berkeley Co.*, 20.0 mi. W Moncks Corner, along SC hwy. 27, 10.0 mi. N jct. I-26, bluff area of Four Holes Swamp Sanctuary, 4M, 2F, 9 September 1980 (NCSM A3493).

Remarks. — The *in situ* gonopodal configuration in this and other species of *Croatania* is the parallel arrangement shown in Figure 46.

Sigmoria (Croatania) yemassee (Shelley), new combination

Croatania yemassee Shelley, 1977:319-321, Figs. 6, 10, 15.

Sigmoria yemassee is still known only from the two collections cited in 1977. I have extensively surveyed the environments in southeastern South Carolina and visited the type locality twice and the other site once at the

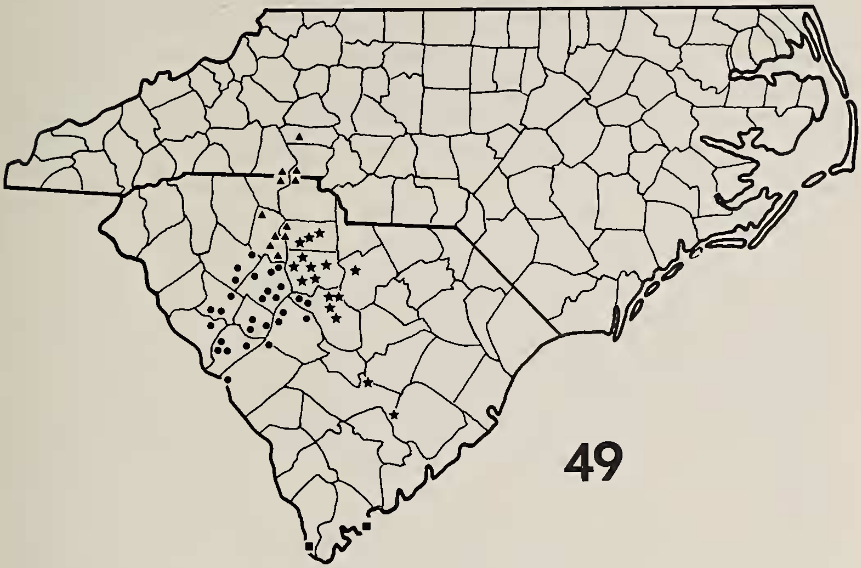


FIG. 49. Distribution of the subgenus *Croatania* in North and South Carolina. Triangles, *catawba;* stars, *simplex;* dots, *saluda;* squares, *yemassee.*

proper times of the year, without finding a single individual. The color in life is therefore unknown.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on distal extremity of basal zone and proximal part of distal zone; gonopods with following diagnostic characters: prefemoral process large, bisinuately curved, bent ventrad apically and narrowing to acuminate tip, extending to level of distal zone; acropodite thick and heavy, arch high and narrowly rounded, extending just beyond level of prefemoral process; basal zone slightly expanded, with small denticulations on proximomedial edge, not noticeably expanded; anterior bend poorly defined, peak rounded, short and high, apical curve well defined; distal zone very short, angling into arch, apically blunt; medial flange in two parts, a narrow, inconspicuous lamina on distal extremity of basal zone and narrow, rhomboidal projection on distal extremity of peak, representing distal lobe of flange in *catawba;* lateral flange a short quadrate lobe on distal zone, margin finely serrate.

Color in Life. — Unknown.

Holotype Gonopods. — Prefemoral process upright, bisinuately curved, not globose basally, bent ventrad apically and narrowing abruptly to acuminate tip; latter directed toward midpoint of telopodite. Acropodite moderately thick and heavy, well sclerotized; arch high and narrowly rounded, upright, slightly overhanging prefemoral process; basal zone without ridge, proximomedial expansion short, with only small denticulations, none enlarged; anterior bend poorly defined; peak short, apex at midlength; apical curve sharp, well defined; distal zone short, projecting inward for short distance into arch, tip broadly rounded and directed toward basal zone. Medial flange located on distal extremity of basal zone and proximal part of distal zone; former a short, narrow, inconspicuous lamina; latter a linear rhomboidal projection. Lateral flange represented by quadrate lobe, margin finely serrate. Prostatic groove crossing from medial to lateral sides at midlength of basal zone, continuing to subterminal opening.

SIGMORIA (CLEPTORIA) Chamberlin, new status

Cleptoria Chamberlin, 1939:9. Chamberlin and Hoffman, 1958:28. Hoffman, 1967:5-7; 1979:158. Jeekel, 1971:254.

Brevigonus Shelley, 1980a:32-34; 1981b:54-55. **NEW SYNONYMY.**

Type species. — Of *Cleptoria, C. macra* Chamberlin, 1939, by original designation; of *Brevigonus, Cleptoria shelfordi* Loomis, 1944, by original designation.

Diagnosis. — Paranota red, metaterga either uniformly black or with conclorous red stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture, inserting between 7th legs; prefemoral process moderate to small, frequently absent; acropodites moderately thick to massive, heavily sclerotized, oriented normally on coxa; basal zone with or without variable basal spine on outer surface; medial flange variable in shape and location, moderately laminate to a thickened swelling of medial surface of acropodite stem, located on basal zone and/or peak, occasionally with suggestion of distal lobe; lateral flange occasionally laminate but usually swollen, thickened, and lobe-like, poorly demarcated from acropodite stem, located more ventrad than laterad, forming highest point of acropodite arch; tip variable.

Remarks. — *Cleptoria* occurs chiefly in piedmont South Carolina and Georgia, and its species have the largest bodies and the most massive, heavily sclerotized acropodites in the genus. The medial flanges are usually thick, stiff projections instead of thin, flexible lamellae as in other subgenera. Likewise, only one species has a laminate lateral flange; otherwise the structure is a swollen, broadly rounded, and poorly demarcated lobe on the proximal part of the distal zone. It typically projects ventrad more than laterad and forms the highest point of the acropodal arch. The distal zone is long and blade-like in one species and is absent from another. In forms with lobe-like lateral flanges, the region is short, broad, and directed perpendicularly from the peak, imparting an overall "bird's head" appearance to the acropodite (Bollman 1888).

Cleptoria presents the most difficult taxonomic decisions in *Sigmoria s. lat.*, particularly with the highly variable South Carolina forms. Central and southern populations of *macra* possess sharply acute spurs on the outer surfaces of the peaks as do adjacent populations of *shelfordi,* the parapatric southern form with a shortened acropodite (lacking the distal zone and apical curve). This condition could derive from that in *macra* by reduction of the lateral flange (lobe) and the short distal zone, but the picture is complicated by the random absence of the spur in *shelfordi.* Additionally, random males of *shelfordi* have spines on the basal zones, which are absent from *macra.* Thus, two principal variants of *shelfordi* exist (Shelley 1980a). Its range is unequally divided by *arcuata,* which has a long distal zone and basal acropodal spine. *Sigmoria (Cleptoria) robusta,* with a swollen, rounded lateral flange and a short distal zone, occurs west of *arcuata.* Its acropodite is heavier than that of *macra* and is similar to the Georgia species; it also lacks the spur but has the basal spine. Thus in South Carolina, forms with shortened acropodites (the variants of *shelfordi*) connect forms with "bird's head" acropodites (*robusta* and *macra*), which in turn are segregated elsewhere by a form with a long curved distal zone (*arcuata*) that also bisects the range of the first form (*shelfordi*)! Features like the basal spine and midlength spur traverse the sharp boundaries between the overall acropodal forms. The spine occurs in *robusta, arcuata,* and randomly in *shelfordi;* the spur also occurs randomly in *shelfordi* and in all populations of *macra* except the northern ones.

The picture is clearer in Georgia because there is only one acropodal form, the "bird's head." Hoffman (1967) recognized three species, and I concur although the status of *bipraesidens,* known only from the holotype, could change when more material is available from northwest of Athens. Unlike the parapatric *rileyi, bipraesidens* lacks the spine on the basal zone; has a longer, more acute, and more strongly indented distal zone; and the entire medial surface of the peak is thickened to represent the flange. *Sigmoria (Cleptoria) abbotti,* the parapatric species to the east of *rileyi,* is most common along the Savannah River between Hart and Burke counties. It differs from *rileyi* in having a prefemoral process; an expanded, laminate anterior margin of the basal zone; a thin, narrow, indistinct medial flange; and a stronger basal spine. Similarities in the basal zones and prefemora of *abbotti* and *robusta* suggest prior connection and that the ancestral range curved northward from Hart County. Following segregation by the Savannah River, the forms diverged as revealed by the outer margins of the distal zones, rounded and continuous in *robusta* and strongly indented in *abbotti.* Thus, the "bird's head" acropodal configuration and the spine on the basal zone traverse the Savannah River, whereas the spur, the short acropodite of *shelfordi,* and the long curved one of *arcuata* are restricted to the northern side. The last three conditions evolved subsequent to the "bird's head" configuration, which antedates the present course of the Savannah River. Equally interesting are small, allopatric populations of *rileyi* in eastern and central Alabama. Reasonably thorough searches have failed to produce *rileyi* in western Georgia, and the main range is disjunct from that in eastern Alabama by about 100 miles. Thus, geographical isolation brought about by the Savannah River seems to have promoted divergence of *robusta* and *abbotti,* which are only about 20 miles apart, but isolation has not affected the Alabama populations of *rileyi,* which are also segregated by major waterways and five times as much distance!

A complete description is presented for *robusta,* but only diagnoses and color statements are provided for *shelfordi* and *arcuata,* since their gonopods were characterized in "sigmoid" terminology by Shelley (1980a, 1981b). Hoffman (1967) published full descriptions for *rileyi, abbotti, bipraesidens,* and *macra,* so only diagnoses, color statements, and redescriptions of the gonopods are needed. The species of *Cleptoria* form a homogeneous unit, and thus there is only one, the *rileyi,* species group.

Components. — *rileyi* (Bollman), *macra* (Chamberlin), *shelfordi* (Loomis), *bipraesidens* (Hoffman), *abbotti* (Hoffman), *arcuata* (Shelley), *robusta* new species.

Sigmoria (Cleptoria) rileyi (Bollman), new combination Figs. 50-52

Fontaria rileyi Bollman, 1888:345. Attems, 1938:167.
Cleptoria rileyi: Chamberlin, 1939:10. Chamberlin and Hoffman, 1958:28.
Cleptoria rileyi rileyi: Hoffman, 1967:12-15, Figs. 2, 7-8.
Cleptoria rileyi alabama Hoffman, 1967:16-17, Figs. 9-10. **NEW SYNONYMY.**

Hoffman (1967) provided a detailed description and illustrations of the holotype of *rileyi* along with a short account of the allopatric population in Lee County, Alabama. Toward the end of the present study a nearly identical male was obtained from Jefferson County, about 100 miles northwest of Lee County. I find no meaningful differences between the Alabama forms and those in central Georgia and no justification for taxonomic recognition. The following supplemental account characterizes the sternal process of the holotype and its gonopods in "sigmoid" terminology, and addresses aspects of variation, ecology, and distribution. I also present additional drawings of the gonopods including one from ventral view, which shows the flange protruding on the medial side.

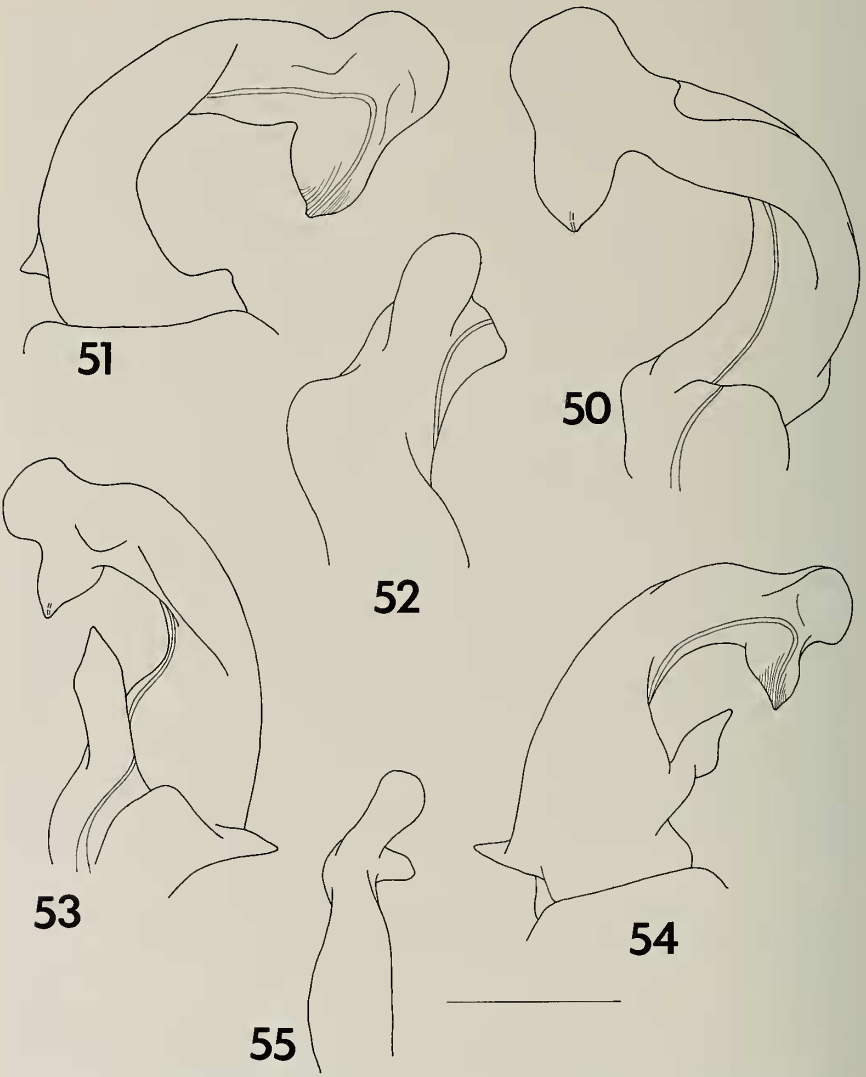
Type specimens. — Male holotype (NMNH) collected by L.M. Underwood, August 1887, at Macon, Bibb Co., GA.

Diagnosis. — A large species of *Sigmoria* with medial flange on peak and with red paranota, metaterga without stripes; gonopods with following diagnostic characters: prefemoral process absent; acropodite massive, arch flattened and squared, extending well beyond level of prefemur; basal zone moderately long and broad, with small basal spine on caudal edge; anterior bend well defined; peak long, flat, constricted distad; apical curve well defined; distal zone short, directed perpendicularly from peak, outer margin moderately indented, sides narrowing apically to subacuminate tip; medial flange thick but relatively laminate, arising on proximal portion of peak, expanding into broadly rounded distal lobe near midlength of peak; lateral flange represented by thick, broadly rounded lobe on proximal part of distal zone, protruding ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life. — Paranota red; metaterga dark glossy black, without stripes along caudal edges; collum also without stripes along either margin.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae (Hoffman, 1967, Fig. 2).

Gonopods *in situ* with acropodites projecting anteriad from aperture, extending forward in parallel arrangement over anterior margin to between 7th legs. Gonopod structure as follows (Figs. 50-52): Prefemoral process absent. Acropodite massive, heavily sclerotized, forming rectangular arch overhanging and extending well beyond prefemur; basal zone moderately broad, anterior edge slightly thinner than caudal but not especially laminate or expanded, outer margin wider basally with short spiniform projection; anterior bend sharp, well defined, approximately a right angle; peak relatively long, straight, and level, constricted on both margins at distal extremity; apical curve sharp, well defined; distal zone short, with distolateral striae, outer margins moderately indented, margins gently curved and narrowing to blunt tip; latter directed toward coxa. Medial flange relatively thick, moderately laminate, arising proximally



Figs. 50-55. 50-52, *Sigmoria (Cleptoria) rileyi.* 50, telopodite of left gonopod of holotype, medial view. 51, the same, lateral view. 52, the same, ventral view. 53-55, *Sigmoria (Cleptoria) abbotti.* 53, telopodite of left gonopod of male from Lincoln Co., GA, medial view. 54, the same, lateral view. 55, the same, ventral view. Scale line = 1.00 mm for all figures.

on peak, curving sharply mediad and forming broadly rounded lobe near midlength of peak, terminating abruptly distal to lobe. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad forming highest point of acropodite arch, poorly demarcated from acropodite stem by only slight impression in distal zone. Prostatic groove crossing to lateral side at anterior bend, curving onto distal zone and opening terminally.

Variation. — Gonopodal variation in *rileyi* is negligible. Males from central Georgia are nearly identical to each other, and the only difference in those from Alabama is a slight enlargement on the anterior surface of the prefemur in some individuals, which suggests a vestigial prefemoral process.

Ecology. — *Sigmoria (Cleptoria) rileyi* occurs under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — Comprised of three allopatric populations, one in central Georgia, and one in Lee and one in Jefferson counties, Alabama (Fig. 68). These areas are in the Piedmont Plateau, the Fall Zone, and the Cumberland Plateau, respectively. The Georgia population occupies a linear area roughly 60 miles long between I-85 and I-75, and three trips to sections of Georgia west of that shown in figure 68 produced specimens of *Dynoria medialis* Chamberlin and *Sigmoria (Cheiropus) persica,* but none of *rileyi.* At best the species is uncommon here. Material was examined from the following new localities:

GEORGIA. — *Clarke Co.,* Athens, 3M collected in June, July, and October 1948-1972 (FSCA). *Oconee Co.,* Bogart, 2M, 14 October 1973, R.L. Duffield (RLH). *Morgan Co.,* Hard Labor Creek St. Pk., 4M, 3F, 15 June 1958, N.B. Causey (FSCA). *Putnam Co.,* 7 mi. S Eatonton, Sinclair Lake Rec. Area, Oconee Nat. For., M, 20 November 1977 (NCSM A1786); and 7 mi SE Monticello, along GA hwy. 212 at Jasper co. line, 3M, 20 November 1977 (NCSM A1788).

ALABAMA. — *Lee Co.,* Chewacla St. Pk., 7M, 4F, 21 May 1980 (NCSM A3122); Auburn, 8M, 13 June 1959, N.B. Causey (FSCA) and Auburn Univ. campus, 2M, June-July 1973, F.M. Scale and R. Russell (AU). *Jefferson Co.,* 10 mi. S Birmingham, along AL hwy. 150, 1.2 mi. W jct. US hwy. 31, M, Fall 1984, R.E. Ashton (NCSM A4228).

Sigmoria (Cleptoria) abbotti (Hoffman), new combination Figs. 53-55

Cleptoria abbotti Hoffman, 1967:18-21, Figs. 13-16.

This species was known from only two localities when it was described and illustrated by Hoffman (1967). Much more material is available now, providing insight into variation and distribution. The lateral flange, which Hoffman called the subapical lobe, seems overemphasized in his drawings, and I therefore present figures of a male from Lincoln County, Georgia, approximately 55 miles NW of the type locality.

Type specimens. — Male holotype (NMNH) and one male and one female paratype collected by L. Hubricht, 22 May 1960, from 5 mi. SW Waynesboro, Burke Co., GA. Male and female paratypes deposited in RLH.

Diagnosis. — A large species of *Sigmoria* with medial flange extending from distal extremity of basal zone to midlength of peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: projection of prefemur present, either distinct process or fold of anterior lamina of basal zone; acropodite massive, leaning over and extending beyond level of prefemoral process; basal zone very broad, inner surface convex with thin, laminate lateral margin and with short, acute, basal spine on caudal margin; anterior bend poorly defined; peak short; apical curve well defined; distal zone short, directed perpendicularly from peak, outer margin strongly indented, sides tapering to subacuminate tip; medial flange thick, narrow, and inconspicuous, not particularly laminate, terminating in slight lobe on distal part of peak; lateral flange represented by thick, broadly rounded lobe on proximal portion of distal zone, protruding ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life. — Paranota red; metaterga dark glossy black, without stripes along caudal edges; collum also without stripes.

Holotype. — 4th sternal process long, apically divided, longer than widths of adjacent coxae (Hoffman 1967, Fig. 4).

Gonopods *in situ* with acropodites projecting anteriomediad from aperture, overlapping in midline and extending forward over anterior margin to between 7th legs. Gonopod structure as follows (Figs. 53-55): Prefemur with rounded lobe on medial surface; prefemoral process short and conical, directed toward apical curve. Acropodite massive, heavily sclerotized, leaning over and extending well beyond level of prefemoral process; basal zone broad, with short, acute spine proximad on outer margin, medial surface convex with anterior edge expanded into thin lamina; anterior bend broad, poorly defined; peak short and thick; apical curve sharp, well defined; distal zone short, with distolateral striae, outer margins gently curved and narrowing to subacuminate tip; latter directed toward coxa. Medial flange thick, narrow, and inconspicuous, arising on basal zone, terminating at midlength of peak, latter with slight thickening on medial surface distal to flange representing lobe of latter. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad, leaning laterad and demarcated from distal zone by slight depression. Prostatic groove crossing to lateral side at anterior bend, curving onto distal zone and terminating apically.

Variation. — The anterior edge of the basal zone is thin and laminate, and in many males, what is called the prefemoral process is really just the expanded, folded proximal end of this lamina, which appears as a separate projection because its profile is viewed in medial perspective. Few males in addition to the types have a truly separate subconical process (Hoffman 1967) that extends clearly beyond the margin of the lamina. The structure occurs randomly throughout the range, being found on males from Hart, Elbert, Lincoln, and Burke counties. The medial flange, inconspicuous in all specimens, also varies randomly. There is a slight thickening of the medial surface of the peak at the level of the apical curve, which is not really visible in medial view and is best seen from the ventral perspective. As in *rileyi,* I think this represents the distal lobe of the medial flange, and it is continuous with the medial flange in males from Columbia County. The size of the spine on the outer surface of the basal zone also varies, but the projection on the 4th sternum is longer than the widths of the adjacent coxae in all individuals.

Ecology. — *Sigmoria (Cleptoria) abbotti* is typically found in predominantly hardwood areas under thin layers of leaves on relatively hard substrates near water sources. I also encountered it in similar spots in predominantly pine woods, under the few deciduous trees in the area.

Distribution. — The Piedmont Plateau and the inner edge of the Coastal Plain along the southern side of the Savannah River from Hart to Burke counties, Georgia. The area is about 85 miles long, but *abbotti* is most common between US highways I-85 and I-20. It extends to 30 miles south of the river, there abutting the range of *rileyi* (Fig. 68). Material was examined from the following new localities:

GEORGIA. — *Oconee Co.,* Watkinsville, M, F, 26 March 1959, W. Tarpley (FSCA). *Hart Co.,* 8 mi. ESE Hartwell, along co. rd. 1724 at Little Cedar Cr., 2M, 20 July 1979 (NCSM A2841). *Elbert Co.,* 11 mi. NNE Elberton, along GA hwy. 368 at Pickens Cr., 2M, F, 20 July 1979 (NCSM A2840); Nancy Hart St. Pk., M, F, 19 July 1979 (NCSM A2938). *Oglethorpe Co.,* Oconee Nat. For., 3M, 8 June 1973, R.L. Duffield (RLH). *Greene Co.,* 10.8 mi. NW Greensboro, Oconee R. Rec. Area, Oconee Nat For., 2M, F, 22 November 1977 (NCSM A1799). *Lincoln Co.,* 6 mi. N. Lincolnton, along GA hwy. 79 at Mills Cr., 4M, F, 19 July 1979 (NCSM A2835); 2.6 mi. NW Lincolnton, along GA hwy. 904 at Soap Cr., 2M, F, 19 July 1979 (NCSM A2832); and 6 mi. SE Lincolnton, along GA hwy. 220 at Cherokee Cr., M, 2F, 19 July 1979 (NCSM A2830). *Columbia Co.,* Mistletoe St. Pk., 2M, F, 18 July 1979 (NCSM A2825); 10 mi. NE Appling, along US hwy. 221 at Clark Hill Dam, 2M, F, 19 July 1979 (NCSM A2828); 15.5 mi. N. Harlem, along GA hwy. 104, 5M, 19 July 1979 (NCSM A2829); 10 mi. NW Augusta, along GA hwy. 28, 0.1 mi. E Savannah R., 2M, F, 13 September 1980 (NCSM A3513); and Augusta Canal St. Pk., 3M, 13 September 1980 (NSCM A3511).

Remarks. — The female from Lincoln County, assigned to *rileyi* by Hoffman (1967), is here referred to *abbotti,* the only species in this county.

Although similar, I think that *abbotti* and *rileyi* are reproductively isolated because parapatric populations in Oconee, Morgan, Greene, and Oglethorpe counties maintain their respective identities and show no evidence of hybridization. *Sigmoria (Cleptoria) abbotti* has a prominent basal spine on the outer surface of the basal zone, whereas that in *rileyi* is barely detectable. The anterior margin of this section, expanded and laminate in *abbotti* is enlarged in some males to represent the prefemoral process. *Sigmoria (Cleptoria) rileyi,* however, lacks both the lamina and a prefemoral process; its medial flange is also more distinct and laminate than that of *abbotti.*

Sigmoria (Cleptoria) bipraesidens (Hoffman), new combination Figs. 56-59

Cleptoria bipraesidens Hoffman, 1967:16-17, Fig. 11

Hoffman (1967) provided a brief description of the holotype and only known specimen of this species, but he did not illustrate the process of the 4th sternum nor show a medial view of the gonopods. I therefore present these figures along with lateral and ventral views of the gonopods and selected anatomical details. No additional material is available to provide information on variation or distribution.

Type specimen. — Male holotype (NMNH) collected by L. Hubricht, 4 April 1953, at Jefferson, Jackson Co., GA.

Diagnosis. — A large species of *Sigmoria* with thickening on medial surface of peak representing medial flange and with red paranota and transverse metatergal stripes; gonopods with following diagnostic characters: prefemoral process absent; acropodite massive, arch flattened and extending well beyond level of prefemur; basal zone without trace of spine on outer surface; anterior bend broad, poorly defined; peak relatively long, flat; apical curve well defined; distal zone moderately long, outer margin strongly indented, directed perpendicularly from peak, inner edge linear, outer edge converging to acuminate tip; medial flange non-laminate, a thickening on peak, narrowest along inner surface and widest on outer; lateral flange represented by thick, broadly rounded lobe on proximal part of distal zone, protruding ventrad, demarcated from acropodite stem by impression on lateral surface.

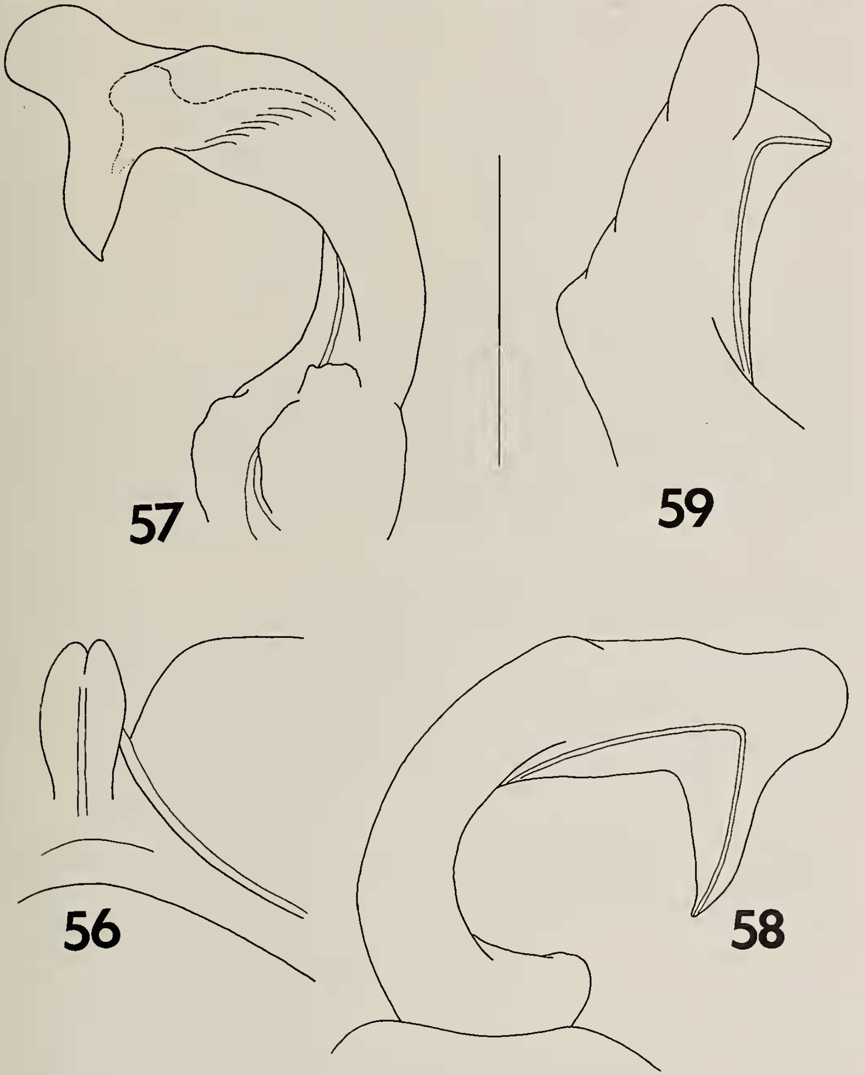
Color in Life (Hoffman 1967). — Paranota red; metaterga black with red transverse stripes along caudal edges; collum with red stripes along both anterior and posterior margins.

Holotype. — Width across genal apices 4.9 mm; genae with distinct central impressions. Facial setae with epicranial, interantennal, genal, and frontal series absent; clypeal about 12-12, labral about 16-16.

Terga smooth, polished, becoming moderately coriaceous on paranota. Latter moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 8, blunt on 9-14, becoming progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surfaces; ozopores located near midlength, opening dorsolaterad.

Sternum of segment 4 with large, apically divided process between 3rd legs, longer than widths of adjacent coxae (Fig. 56); that of segment 5 with two long, paramedial, basally coalesced knobs between 4th legs, length equal to widths of adjacent coxae, and low, flattened, elevated areas between 5th legs; that of segment 6 with shallow, convex, depression between 7th legs to accommodate curvatures of acropodites. Coxae with low, blunt tubercles arising on postgonopodal legs of segment 9, becoming sharper and more acute posteriorly; prefemoral spines arising on segment 5, becoming longer and sharper caudally.

Gonopodal aperture ovoid, 4.4 mm wide and 2.7 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. *In situ* arrangement of gonopods



Figs. 56-59. *Sigmoria (Cleptoria) bipraesidens.* 56, process of 4th sternum of holotype, caudal view. 57, telopodite of left gonopod of the same, medial view. 58, the same, lateral view. 59, the same, ventral view. Scale line = 1.00 mm for 56 and 59; 1.60 mm for 57-58.

unknown. Gonopod structure as follows (Figs. 57-59): prefemoral process absent. Acropodite thick and massive, heavily sclerotized, forming rectangular arch, overhanging and extending well beyond prefemur; basal zone moderately broad, without spine on outer surface, with short blunt, basal lobe on medial side; anterior bend sharp, well defined, approximately a right angle; peak relatively long, straight, and level, constricted very slightly on both margins on distal extremity; apical curve sharp, well defined; distal zone moderately long, directed perpendicularly from peak, outer margin strongly indented, inner edge linear, outer straight proximally then curving beyond midlength and converging with inner at acuminate tip; latter directed toward coxa. Medial flange represented by thickened non-laminate area along entire width of peak, beginning proximally and terminating on distal extremity, narrowest on inner margin, widest on outer. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad forming highest point of acropodite arch, leaning slightly laterad and demarcated from distal zone by slight depression. Prostatic groove crossing to lateral side at anterior bend, bending sharply (90°) onto distal zone and opening terminally.

Remarks. — The striped color pattern of *bipraesidens* (Hoffman 1967) should be confirmed in fresh material, since this is the only reported individual in *Cleptoria* with metatergal markings.

The differences between *bipraesidens* and *rileyi* are even less distinct than those between the latter and *abbotti*. However, their close geographical proximity combined with the longer distal zone and non-laminate medial flange of *bipraesidens* suggest reproductive isolation. The status of *bipraesidens* should be reviewed when more material is available.

Sigmoria (Cleptoria) robusta Shelley, new species Figs. 60-63

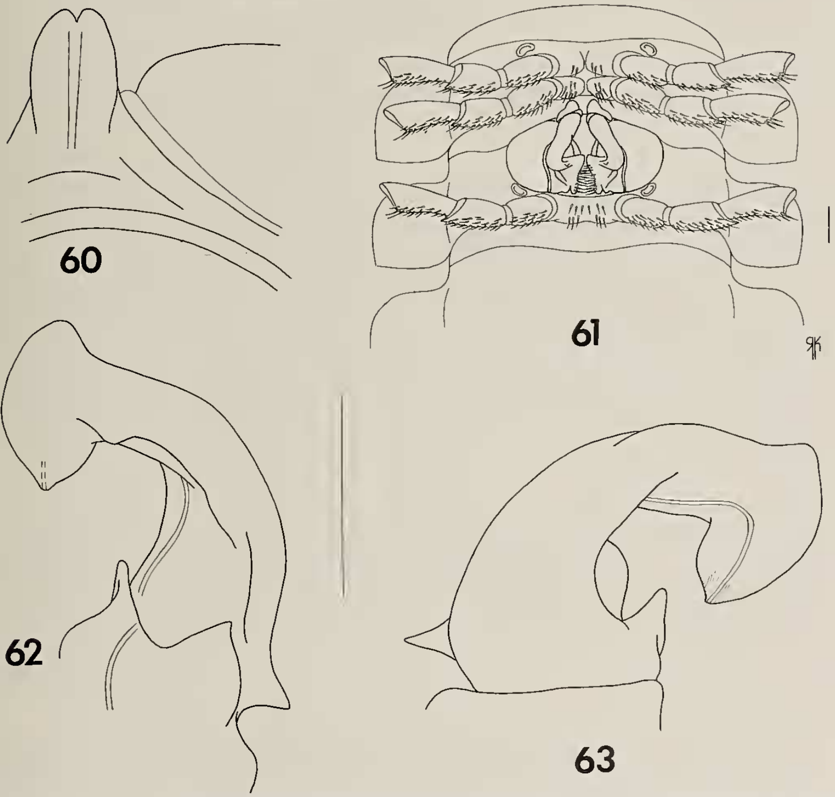
Type specimen. — Male holotype (NCSM A1553) and one male and one female paratypes collected by R.M. Shelley, 7 May 1977, in Oconee Co., SC, 10.8 mi. SW Seneca, along SC highway 168, 0.3 mi. S junction with SC highway 86. Male and female paratypes (NCSM A2061) collected by R.M. Shelley and W.B. Jones, 10 June 1978, in Oconee Co., 5.7 mi SE Oakway, along SC highway 66 at Beaverdam Cr. SC. Male paratype deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* with medial flange extending between distal extremity of basal zone and proximal portion of distal zone and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process short, blunt, and narrow; acropodite massive, arch flattened and extending beyond level of prefemoral process; basal zone very broad, inner surface convex and lateral margin thin and laminate, with sharply acute basal spine on caudal edge; anterior bend broad, poorly defined; peak flattened but rising to distal apex; apical curve sharp well defined; distal zone short, directed perpendicularly from peak, outer margin not indented, sides curving broadly to blunt tip; medial flange thick but relatively laminate, long, narrow, and inconspicuous, with broadly rounded distal lobe; lateral flange represented by thick broadly rounded lobe on proximal part of distal zone, produced ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life. — Paranota red; metaterga black, without stripes along caudal margins; collum without stripes along either margin.

Holotype. — Length 48.3 mm, maximum width 11.4 mm, W/L ratio 23.6%, depth/width ratio 58.8%. Segmental widths as follows:

collum	7.7 mm	14th	11.2
2nd	9.1	15th	10.8
3rd	9.8	16th	10.2
4th	10.6	17th	8.9
5th-7th	10.9	18th	6.4
8th-13th	11.4		



FIGS. 60-63. *Sigmoria (Cleptoria) robusta.* 60, process of 4th sternum of holotype, caudal view. 61, gonopods *in situ,* ventral view of paratype. 62, telopodite of left gonopod of holotype, medial view. 63, the same, lateral view. Scale line for fig. 61 = 1.00 mm; line for other figs. = 1.00 mm for 62-63; 1.33 mm for 60.

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 1.5 mm, interantennal isthmus 1.9 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres 2 > 3 > 6 > 4 = 5 > 1 > 7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, genal, and frontal absent, clypeal about 11-11, labral about 16-16.

Terga smooth, polished, becoming coriaceous on paranota. Collum broad, ends extending well below those of adjacent tergite. Paranota moderately depressed, containing slope of dorsum, caudolateral corners rounded through segment 5, blunt on segments 6-11, becoming progressively more acute posteriorly. Peritremata sharp and distinct, strongly elevated above paranotal surface; ozopores located near midlength, opening dorsolaterad.

Sternum of segment 4 with large, apically divided process between 3rd legs, much longer than widths of adjacent coxae (Fig. 60); that of segment 5 with two medially coalesced knobs between 4th legs and longer, more separate projections between 5th legs, latter equal in length to widths of adjacent coxae; sternum of segment 6 without depression on caudal edge, with two rounded, elevated areas between 7th legs, shorter than widths of adjacent coxae. Postgonopodal sterna with two blunt lobes on caudal edge of segment 8 arising from bicruciform impression; segment 9 also with bicruciform impression but flattened between caudal legs; remaining sterna becoming progressively flatter and more plate-like posteriorly, with variably broad, shallow, central impressions. Coxae with low, blunt tubercles arising on segment 9, becoming larger posteriorly; prefemoral spines arising on segment 5, becoming progressively longer and sharper caudally.

Gonopodol aperture elliptical, 4.9 mm wide and 2.4 mm long at midpoint, without indentations, sides flush with metazonal surface. Gonopods *in situ* (Fig. 61, of paratype) with acropodites projecting anteriad from aperture, nearly parallel but angling towards each other and extending slightly beyond anterior margin, not overlapping or touching. Gonopod structure as follows (Figs. 62-63): Prefemur with acutely triangular, ventromedial lobe; prefemoral process blunt and narrow, arising from lamina of basal zone, directed toward apical curve. Acropodite massive, heavily sclerotized, forming rectangular arch, overhanging and extending well beyond level of prefemoral process; basal zone broad, with sharply acute spine basally on outer margin, medial surface convex with anterior edge expanded into thin lamina; anterior bend sharp, well defined; peak moderately long and straight, angling slightly ventrad with apex distad; apical curve sharp, well defined; distal zone short and very broad, outer margin not indented, gently rounded and converging with inner to form blunt tip, with short striations on lateral surface; tip directed toward coxae. Medial flange thick, heavy, and narrow, relatively laminate, arising on distal extremity of basal zone, curving across anterior bend and narrowing on proximal part of peak, then expanding into broadly rounded distal lobe, terminating on proximal part of distal zone. Lateral flange lobe-like, located on proximal part of distal zone, produced ventrad, forming highest point of acropodite arch, poorly demarcated from acropodite stem by slight impression in distal zone, continuous with outer margin of distal zone. Prostatic groove crossing to lateral side at anterior bend, curving onto distal zone and opening terminally.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 41.5 mm, maximum width 9.9 mm, W/L ratio 23.9%, depth/width ratio 63.6%. Agreeing closely with males in somatic features, except ends of collum not produced beyond those of following tergite. Cyphopods *in situ* with corner of receptacle and valves visible in aperture, latter directed caudolaterad. Receptacle large, cupped around medial side of valves, with ridges and lobes, surface rugulose. Valves large, equal, surfaces finely granulate.

Variation. — Except for slight changes in the length and shape of the prefemoral process and the spine on the basal zone, the gonopods in this species are essentially uniform. Likewise, all males possess elevated areas on the 6th sternum between the 7th legs and lack a depression at this point.

Ecology. — *Sigmoria (Cleptoria) robusta* occurs under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — The Piedmont Plateau in the western corner of South Carolina between the Toxaway and Chatooga Rivers. The species extends to the base of the Blue Ridge Escarpment but apparently is absent from the mountains. Specimens were examined as follows:

SOUTH CAROLINA. — *Oconee Co.,* 7.1 mi. NE Walhalla, along SC hwy. 24 at Little R., M, 7 May 1977 (NCSM A1557); 4.8 mi. W Seneca, along SC hwy. 13 at Corneross Cr., 2F, 7 May 1977 (NCSM A1554); 5 mi. S Seneca, along SC hwy. 54 at Hartwell Res., 2M, 7 May 1977 (NCSM A1555); 10.8 mi. SW Seneca, along SC hwy. 168, 0.3 mi. S jct. SC hwy. 86, 2M, F, 7 May 1977 (NCSM A1553) TYPE LOCALITY; and 5.7 mi. SE Oakway, along SC hwy. 66 at Beaverdam Cr., M, F, 10 June 1978 (NCSM A2061). *Anderson Co.,* 10.3 mi. SW Pendleton, along SC hwy. 192 at Beaverdam Cr., M, 4F, 7 May 1977 (NCSM A1552).

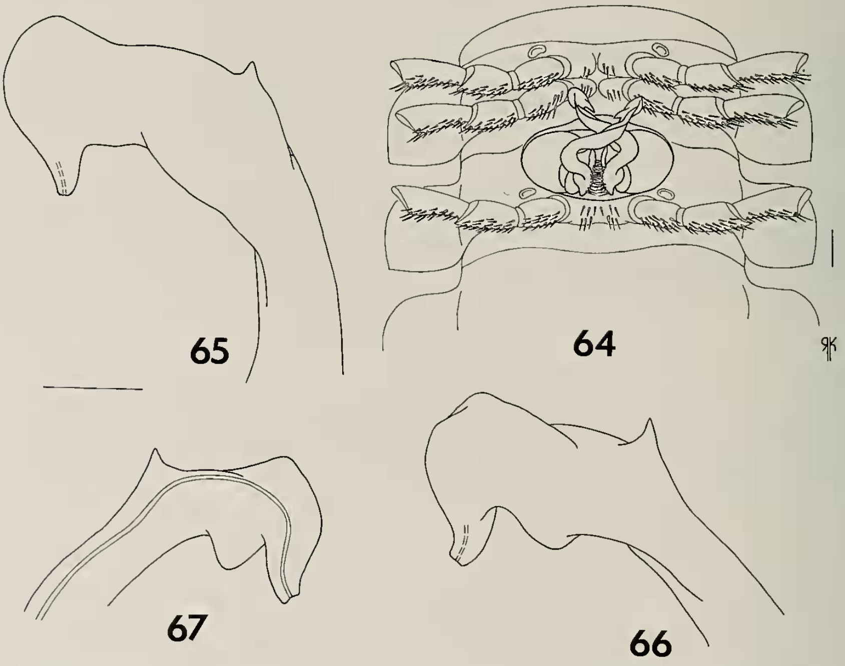
Remarks. — *Sigmoria (Cleptoria) robusta* shares ancestry with *abbotti* and represents a population that became isolated north of the Savannah River. They are similar in the narrow medial flanges and the expanded, laminate anterior margins of the basal zones that lead into the prefemoral processes. However, the spine on the basal zone is larger in *robusta,* and there is a distinct distal lobe on its medial flange instead of a thickening or boss as in *abbotti.* Another difference obtains on the 6th sternum, which is moderately depressed between the 7th legs in *abbotti* and displays two elevated lobes in *robusta.*

Sigmoria (Cleptoria) macra (Chamberlin), new combination Figs. 64-67

Cleptoria macra Chamberlin, 1939:9, pl. 4, Figs. 36-37. Chamberlin and Hoffman, 1958:28. Hoffman, 1967:7-11, Figs. 3, 5, 6, and 12.
Cleptoria rileyi Loomis, 1943:402.

Hoffman (1967) presented a detailed description of *macra,* and his medial gonopodal illustration shows the medial flange arising on the basal zone and terminating on the peak. The flange in *macra* is thus in the same position as those in *shelfordi* and *arcuata* (Shelley 1980a, 1981b) and a close relationship is confirmed by new material with a spur on the outer surface of the acropodite at the anterior bend (Figs. 65-67). This spur is homologous to that in *shelfordi,* leaving no doubt that the species are congeneric. Loomis understood this fauna better than any subsequent author, as he (1944) assigned *shelfordi* to the same genus as *macra,* and (1943) expressed doubts as to the validity of *Cleptoria.*

Diagnosis. — A large species of *Sigmoria* with medial flange extending between midlength of basal zone and distal extremity of peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral processes short and variably triangular; acropodite moderately thick and heavy, arch either flattened or gently rounded, extending only slightly beyond level of prefemoral process; basal zone moderately long, without modifications; anterior bend broad, poorly defined; peak variable, flattened or gently curved, with or without sharply acute spur on outer surface; apical curve well defined; distal zone short, outer margins slightly indented, directed perpendicularly from peak, sides curving and narrowing to blunt tip; medial flange variable in length and configuration, arising on distal extremity of basal zone, terminating from midlength of peak to proximal portion of distal zone, usually with curved



Figs. 64-67. *Sigmoria (Cleptoria) macra.* 64, gonopods *in situ,* ventral view of male from Newberry Co., SC. 65, acropodite of left gonopod of the same, medial view. 66, distal part of acropodite of male from Greenville Co., SC, medial view. 67, the same, lateral view. Scale line for fig. 64 = 1.00 mm; line for other figs. = 1.00 mm for each.

proximal margin, then indented and terminating in rounded or triangular distal lobe; lateral flange a broadly rounded lobe on proximal part of distal zone, protruding ventrad, demarcated from acropodite stem by slight impression on lateral surface.

Color in Life. — Paranota red; metaterga black, without stripes along caudal edges; collum also without stripes along either margin.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae (Hoffman 1967, Fig. 3).

Gonopods *in situ* (Fig. 64, not this specimen) with acropodites crossing at midlength in midline of aperture, extending forward over anterior margin to between 7th legs. Gonopod structure as follows (Hoffman 1967, Figs. 65-67): Prefemoral process short, nearly straight, tapering to acuminate tip, directed toward distal zone. Acropodite thick and heavy, well sclerotized, forming broad, rectangular arch, overhanging and extending slightly beyond level of prefemoral process; basal zone moderately long, without modifications; anterior bend sharp, well defined; peak moderately long, broad, and flattened, rising continuously to apex at distal extremity, with thin curved lamella on outer margin of lateral surface; apical curve sharp, well defined, approximately a right angle; distal zone short, with outer edge slightly indented and angling sharply inward to form blunt tip; latter directed toward coxa. Medial flange relatively broad, thin, and laminate arising on distal extremity of basal zone, curving broadly across anterior bend and terminating on distal extremity of peak. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad, poorly demarcated from acropodite stem by slight depression in lateral surface. Prostatic groove crossing to lateral side at anterior bend, running along outer margin of peak, curving sharply and extending through center of distal zone to terminal opening.

Variation. — I have collected *macra* five times, all south of the type locality, and each male possesses a short acute spur on the outer margin at the anterior bend, or at midlength of the medial flange (Figs. 65-67). Hoffman (1967) did not mention this feature in his account of variation, but my specimens, collected at nearly the same site in Newberry County possess it (Fig. 66). Northern populations evidently lack the spur and are atypical. Males from the center of the range in Greenville County have broadly rounded, nearly triangular lobes distally on the medial flange (Figs. 66-67).

Distribution. — A linear area approximately 60 miles long in piedmont South Carolina, ranging from north of Greenville to the Saluda River in southern Newberry County. Hoffman (1967) predicted that *macra* would probably be found in North Carolina but I have sampled intensively north of the type locality without encountering it. *Sigmoria (Cleptoria) divergens* Chamberlin is common in this area and along the North Carolina-South Carolina state line in the Blue Ridge escarpment. As with *simplex (Croatania),* the type locality is near the northern range limit. Material was examined from the following new localities:

SOUTH CAROLINA. — *Greenville Co.,* 8.7 mi. SW Fountain Inn, along SC hwy. 68 at Reedy Cr., M, 3F, 11 June 1978 (NCSM A2069); and 12.5 mi. SW Fountain Inn, along SC hwy. 51 at Mountain Cr., M, 11 June 1978 (NCSM A2068). *Newberry Co.,* 5.2 mi. N Chappells, along SC hwy. 56, 0.2 mi. N jct. SC hwy. 347, 4M, 2F, 3 May 1977 (NCSM A1523) and M, F, 22 April 1982 (NCSM A3927).

Sigmoria (Cleptoria) shelfordi (Loomis), new combination

Cleptoria shelfordi Loomis, 1944:172-173, Fig. 4. Chamberlin and Hoffman, 1958:28.
Brevigonus shelfordi: Shelley, 1980a:35-41, Figs. 1-13; 1981b:55-56.

Occurring along the northern side of the Savannah River in piedmont South Carolina (McCormick, Abbeville and Oconee counties), *shelfordi* was adequately described in two previous papers (Shelley 1980a, 1981b), the latter characterizing the gonopods in "sigmoid" terminology. Aspects of variation, ecology, and distribution were also discussed. No new records are available.

In the first account (Shelley 1980a) two gonopodal variants were described. Variant A has a basal spine on the outer surface of the basal zone, a large medial flange that partly or completely obscures the acropodite stem in medial view, and a compact curvature with the tip directed toward the coxa. It usually lacks the spur, and the stem is apically entire. Variant B lacks the basal spine, has a narrower medial flange that reveals the prostatic groove to the crossover point, and has a more open curvature with the tip directed generally parallel to the coxa. This form, which includes the type specimens, possesses the spur and is usually apically indented. Occasionally, characters from one form appear in the other (i.e. the spur of B in A, and the apical configuration of A in B), proving that they are not reproductively isolated. Subspecific recognition is also not justified because they occur sympatrically and are interspersed throughout the range. Therefore, *shelfordi* is a polymorphic species. Although the two variants are intermixed in McCormick and Abbeville counties, form A tends to occur more in the west proximal to the ranges of *arcuata* and *robusta,* and form B more in the east and north proximal to *macra.* In form B, absence of the basal spine is shared with *macra,* and presence of a spur is shared with southern populations of *macra.* Since *shelfordi* and *macra* are proximal and lack known intergrades, they are considered separate species even though geographic variation in these features crosses cladistic lines.

I return to *shelfordi* the Oconee County record [Clemson vic., under dead pig, 2M, F, 18 July 1962, J.A. Payne (RLH)], which I (1980a) assigned to it and later (1981b) switched to *arcuata.* This record is troublesome because it is segregated by the range of *arcuata.* The form lacks a prefemoral process and has a stronger basal spine, a broader medial flange, and greater acropodal curvature than the other males of *shelfordi.* The Oconee County population, parapatric with *robusta,* agrees with *arcuata* in lacking a prefemoral process, but despite proximity, this is best considered convergence.

Diagnosis. — A large species of *Sigmoria* with medial flange extending between proximal part of basal zone and distal extremity of peak and with red paranota, metaterga without stripes; gonopods with following diagnostic characters: prefemoral process present or absent, variable; acropodite heavily sclerotized, arch extending only slightly beyond level of prefemoral process; basal zone relatively long, about 2/3 of acropodite length, with or without variable basal spine on outer edge; anterior bend variable; peak about 1/3 of acropodite length, flattened or gently curved, with or without short, acute spur on outer or medial surfaces; apical curve and distal zone absent, acropodite terminating in blunt inner corner of peak, apical edge variable; medial flange thick but laminate, length and configuration variable; lateral flange absent.

Color in Life. — Metaterga red; paranota black without stripes along caudal edges; collum with or without narrow stripe along anterior margin.

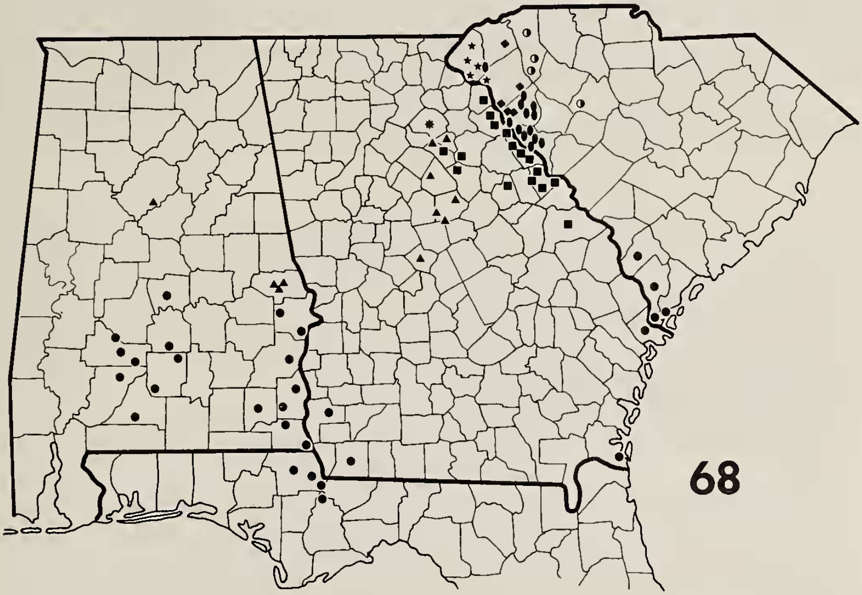


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FIG. 68. Distributions of *australis* and the subgenus *Cleptoria* in the southeastern states. Dots, *australis;* triangles, *rileyi;* squares, *abbotti;* asterisk, *bipraesidens;* stars, *robusta;* diamonds, *arcuata;* ovals, *shelfordi;* half shaded dots, *macra.*

Sigmoria (Cleptoria) arcuata (Shelley), new combination

Brevigonus arcuatus Shelley, 1981b:56-60, Figs. 1-5.

Sigmoria (Cleptoria) arcuata occurs in the Savannah River Valley between the Oconee County locality and all others of *shelfordi.* It ranges northward into Pickens County near the Blue Ridge Front. The previous paper (Shelley 1981b) described *arcuata* in detail and discussed variation, ecology, and distribution. Since no new records are available, I present here only a diagnosis and color statement.

Diagnosis. — A large species of *Sigmoria* with medial flange usually extending between proximal part of basal zone and midlength of peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process absent; acropodite moderately thick, arch a broad curve extending beyond level of prefemur; basal zone with prominent acute spine basally on caudal edge, length variable; anterior bend variable; peak gently curved or flattened; apical curve poorly defined; distal zone moderately long, curving broadly into arch, narrowing smoothly and continuously distally, tip simple or reflexed; medial flange with variable tooth on slightly wider proximal part, then narrowing and either terminating by blending into outer margin of peak or widening again and terminating abruptly at midlength of peak; lateral flange laminate, located on apical curve and proximal part of distal zone.

Color in Life. — Paranota red; metaterga dark glossy black, without stripes along caudal edges; collum also without stripes along either margin.

SIGMORIA (CHEIROPUS) Loomis, new status

Cheiropus Loomis, 1944:170-171. Chamberlin and Hoffman, 1958:25. Jeekel, 1971:253. Hoffman, 1979:159. Shelley 1984a:265-267.
Stelgipus Loomis, 1944:173. Jeekel, 1971:288. Hoffman, 1979:159.
Fontaria: Chamberlin and Hoffman, 1958:33.
Lyrranea Hoffman, 1963:114-115; 1979:159.
Prionogonus Shelley, 1982:460-462. **NEW SYNONYMY.**

Types species. — Of *Cheiropus, C. plancus* Loomis, 1944, by original designation; of *Stelgipus, S. agrestis* Loomis, 1944, by original designation; of *Lyrranea, L. persica* Hoffman, 1963, by original designation; of *Prionogonus, P. haerens* Shelley, 1982, by original designation.

Diagnosis. — Paranota usually red, occasionally orange, metaterga usually with concolorous stripes connecting paranotal markings, rarely uniformly black; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture and inserting between 7th legs; prefemoral process present or absent, moderate when present; acropodites moderately thick and heavy, occasionally massive, well sclerotized, oriented normally on coxa with inner surface directed anteriomediad; basal zone with or without row of spurs on outer surface, occasionally extending onto peak, otherwise unmodified; medial flange present or absent, variable but usually broad and dilated, laminate to thickened, located on peak or distal part of acropodite in forms lacking distal zone; lateral flange present or absent, laminate; distal zone curving either strongly laterad and obscured in medial view by acropodite stem or medial flanges, or replaced by variably positioned solenomerite, latter best revealed in lateral view; tip variable.

Remarks. — The subgenus *Cheiropus,* containing the southernmost apheloriine species, is united chiefly by the laterally directed distal zone or its solenomerite substitute. It lacks geographic cohesion and is divided into four species groups.

The *Australis* group

The *australis* group contains a relatively undifferentiated species in the Coastal Plains of South Carolina, Georgia, Alabama, and Florida. It occurs in three allopatric populations that have not diverged and are unquestionably conspecific.

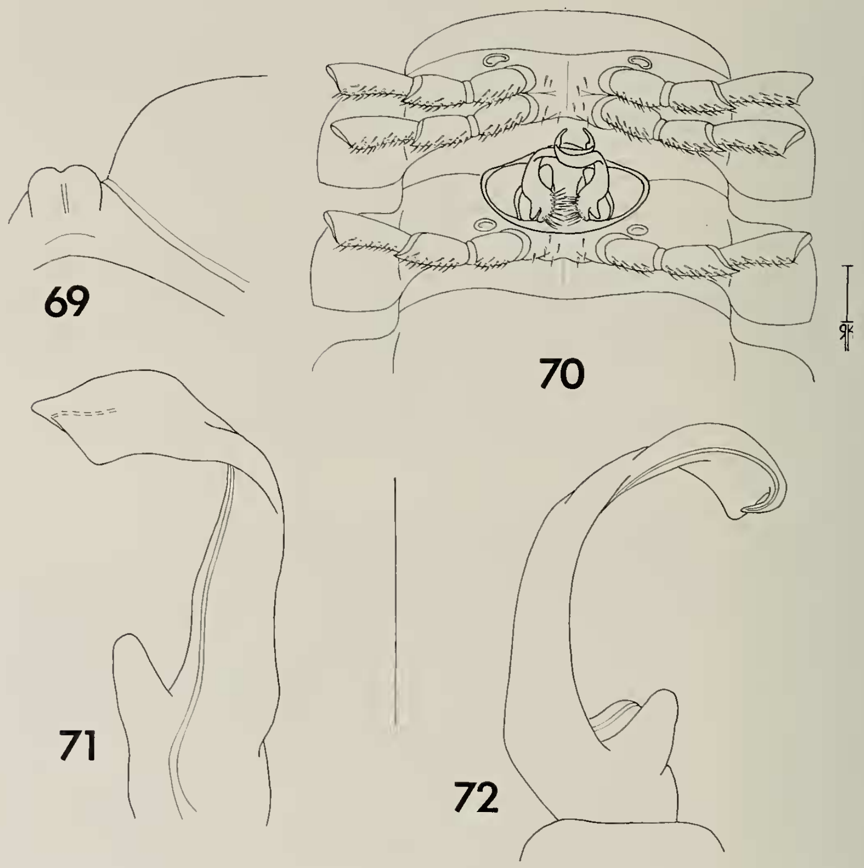
Component. — *australis,* new species

Sigmoria (Cheiropus) australis Shelley, new species Figs. 69-72

Type specimens. — Male holotype (NCSM A2874) and three male and two female paratypes collected by R.M. Shelley and P.T. Hertl, 15 September 1979, from Torreya State Park, Liberty Co., FL. The lushness of this park makes it a popular arthropod collecting site and *australis* has been taken there many times. Too numerous to be cited with complete data, additional paratypes of both sexes are available in the NCSM, FSCA, and WAS.

Diagnosis. — A moderate to large species of *Sigmoria* with medial flange extending between distal extremities of basal zone and peak and with red paranota and variable metaterga, with or without red transverse stripes; gonopods with following diagnostic characters: acropodite moderately thick, arch in form of inverted L, extending slightly beyond level of prefemoral process; basal zone relatively long; anterior bend and apical curve well defined, latter forming arc with narrow diameter, peak short, gently curved; distal zone short, curving laterad from peak, not coplanar with other sections, obscured in medial view by medial flange, sides narrowing to acuminate tip; medial flange relatively long, widening into triangular lamina on distal extremity of peak then terminating abruptly; lateral flange narrow and inconspicuous, located on distal extremity of peak.

Color in Life. — Paranota red; metaterga black, with or without concolorous red stripes along caudal edges connecting paranotal markings; collum with or without red stripes along both margins.



Figs. 69-72. *Sigmoria (Cheiropus) australis.* 69, process of 4th sternum of holotype, caudal view. 70, gonopods *in situ,* ventral view of male from Camden Co., GA. 71, telopodite of left gonopod of holotype, medial view. 72, the same lateral view. Scale line for fig. 70 = 1.00 mm; line for other figs. = 1.00 mm for 71-72, 1.33 mm for 69.

Holotype. — Length 47.3 mm, maximum width 12.8 mm, W/L ratio 27.1%, depth/width ratio 56.3%. Segmental widths as follows:

collum	7.9 mm	7th	12.6
2nd	8.5	8th-14th	12.8
3rd	9.5	15th	12.0
4th	11.0	16th	11.2
5th	12.0	17th	9.7
6th	12.3	18th	6.8

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 5.1 mm, interantennal isthmus 1.8 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres 2 > 3 > 4 > 5 = 6 > 1 > 7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 8-8, labral 14-14.

Dorsum appearing smooth and polished, but moderately coriaceous. Collum broad, ends extending well below those of following tergite. Paranota relatively flat, interrupting slope of dorsum and subparallel to substrate, caudolateral corners rounded through segment 4, blunt on 5-8, becoming progressively more acute posteriorly. Peritremata distinct, sharply elevated above paranotal surface; ozopores located near middle of peritremata, opening dorsolaterad.

Sternum of segment 4 with small process, barely elevated above sternal surface, much shorter than widths of adjacent coxae (Fig. 69); that of segment 5 with two low paramedial knobs between anterior legs and slightly elevated flattened areas between caudal legs; 6th sternum with only slight depression between 7th legs, these set slightly farther apart than 6th legs. Postgonopodal sterna flattened and plate-like, with shallow transverse grooves between leg pairs on segments 8-12 and variably broad, shallow, central impressions on remaining segments. Coxae with low, rounded tubercles beginning on segment 10; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.1 mm wide and 1.3 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 70, not this specimen), with acropodites projecting ventrad from aperture, bending laterad and extending over opposite side in front of and behind each other, curving anteriad with one behind overlapping other and one in front extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 71-72): Prefemoral process short, blunt, directed toward distal zone. Acropodite moderately thick, forming inverted L shaped arch, overhanging and extending slightly beyond level of prefemoral process; basal zone relatively long, unmodified; anterior bend sharp, well defined; peak relatively short, gently curved; apical curve relatively sharp, well defined, forming arc with very narrow diameter; distal zone short, curving laterad from peak, not coplanar with other regions, obscured in medial view by medial flange; tip acuminate. Medial flange arising on distal extremity of basal zone, widening into triangular lamina on distal extremity of peak and terminating abruptly thereafter. Lateral flange a short, narrow, inconspicuous lamella on peak opposite trianglar part of medial flange. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Male Paratypes. — Some male paratypes have more acuminate prefemoral processes, but otherwise all agree closely with the holotype.

Female Paratype. — Length 42.9 mm, maximum width 11.8 mm, W/L ratio 27.5%, depth/width ratio 62.7%. Cyphopods *in situ* with edge of receptacles and opening of valves visible in aperture. Receptacle moderate, situated on medial sides of valves, with ridge on this side, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — Aside from minor changes in the length and bluntness of the prefemoral process and the breadth of the medial flange, the gonopods of *australis* are quite constant throughout the range. Size and color pattern vary, however, and as noted under "Color in Life," individuals may or may not have red stripes along the caudal margins of the metaterga and collum. The types and the sample from Decatur County, Georgia, lack stripes, but as far as one can tell from faded preserved specimens, all others possess them. All the individuals I collected in Alabama, Georgia, and South Carolina were striped.

Regarding size, the types are near maximum for the species. The opposite extreme is found along the Atlantic Coast, as shown by a male from Beaufort County, South Carolina, which measures 29.1 mm in length, 7.4 mm in width, W/L ratio 25.4%, depth/width ratio 53.4%. Large males appear extremely broad in dorsal view, but this is an illusion created by the unusually flat paranota. This effect is less noticeable in small individuals.

Ecology. — Sigmoria (Cheiropus) australis occurs in a variety of mesic deciduous forests under thin layers of leaves on relatively hard substrates, preferably near water sources. In Crooked River State Park, Camden County, Georgia, I found *australis* on sandy-humus soil in a live oak-magnolia forest, but it was absent from the litter of these species occurring instead under other hardwoods. It occurs syntopically with *serrata* at this site, but they are dominant at different times of the year (Shelley 1984a). *Sigmoria (Cheiropus) australis* was more abundant in July 1977 but was absent in October 1980, when *serrata* was present. The life histories therefore seem to be adjusted to minimize ecological competition. A comparable situation may exist in western Georgia at Kolomoki Mounds State Park, Early County, where *australis* and *Dynoria medialis* Chamberlin occur syntopically in typical climax piedmont forest. I have visited this locality twice and found them to be equally abundant in November 1977, whereas *D. medialis* was more common in May 1983.

Distribution. — The Coastal Plains of Alabama, Georgia, southern South Carolina, and northern Florida, ranging from near the Alabama River to the Atlantic Ocean and extending inland to the edge of the Fall Zone, just crossing the Alabama River northwest of Montgomery. The distribution spans several large rivers including the Chattahoochee, Altamaha, and Savannah, but *australis* has not been encountered south of the St. Marys River in Nassau or Duval counties, Florida. As shown in Fig. 68 the available material clusters into three disjunct areas — the Atlantic coast from Hampton County, South Carolina, to Camden County, Georgia; along both sides of the Chattahoochee River from the inner Coastal Plain of Russell County, Alabama, to Liberty County, Florida; and in central Alabama from Autauga to Conecuh counties. There are no anatomical differences between these groups, however, and all are unquestionably conspecific. Additional collecting may eventually connect the two areas in Alabama, but I doubt if the Chattahoochee and Atlantic Coastal populations will ever be connected. Specimens were examined as follows:

ALABAMA: *Autauga Co.,* 2.5 mi. SE Prattville, M, F, 20 August 1960, L. Hubricht (RLH). *Lowndes Co.,* 3 mi. E Braggs, 2F, 4 July 1960, L. Hubricht (RLH). *Wilcox Co.,* along AL hwy. 41, 2.5 mi. S Dallas Co. line, 2M, F, 22 May 1980 (NCSM A3124); 3.5 mi. N Camden, 2M, 11 November 1962, L. Hubricht (RLH); and 2 mi. S Oak Hill, M, 10 May 1960, L. Hubricht (RLH). *Butler Co.,* 3 mi. SE Searcy, 6M, 5F, 9 April 1960, L. Hubricht (RLH); 9.8 mi. NE Greenville, along US hwy. 31 at Pigeon Cr., F, 2 juvs., 21 April 1983 (NCSM A4039); and 3 mi. NW McKenzie, along US hwy. 31, 2M, 2F, 9 April 1960, L. Hubricht (RLH). *Monroe Co.,* 12 mi. NNE Monroeville, along AL hwy. 21, 4.9 mi. N jct. AL hwy. 265, M, 22 April 1983 (NCSM A4046). *Conecuh Co.,* 2.2 mi. SW Evergreen, 10M, 10F, 26 June 1961, L. Hubricht (RLH). *Russell Co.,* 3 mi. N Uchee, 4M, 2F, 12 June 1960, L. Hubricht (RLH); and 14.9 mi. S. Phenix City, along AL hwy. 165, 0.3 mi. N jct. AL hwy. 38, 2F, 26 April 1983 (NCSM A4064). *Barbour Co.,* 13 mi. E Clayton, M, F, 5 September 1959, L. Hubricht (RLH) and 2.7 mi. S Eufaula, along US hwy. 431, 0.5 mi. S jct. AL hwy. 30, F, 29 April 1983 (NCSM A4067). *Henry Co.,* 5 mi. W Capps, M, 6 August 1960, L. Hubricht (RLH) and 2.8 mi. NE Abbeville, along AL hwy. 47, 2.1 mi. E jct. AL hwy. 95, 2F, 29 April 1983 (NCSM A4069). *Dale Co.,* 5.6 mi. NE Ozark, along AL hwy. 105 at Judy Cr., M, 29 April 1983, (NCSM A4071). *Houston Co.,* 4 mi. E Webb, 2F, 9 July 1967, D.R. Whitehead (RLH) and Chattahoochee St. Pk., 4M, 3F, 30 April 1983 (NCSM A4080).

FLORIDA: *Jackson Co,* 5.7 mi. W Greenwood, M, 11 July 1973, R.M. Blaney (FSCA); Florida Caverns St. Pk., several males and females taken in April, May, June, and July from 1957-1975 by various collectors (FSCA, WAS); Marianna, males and females collected from 1961-1970 by various persons (FSCA); Three Rivers St. Pk, 8M, 5F, 19 July 1953, W.A. Shear (WAS); and 3.3 mi. E Sneads, along Appalachicola R., 3M, 2F, 7 September 1959, L. Hubricht (RLH). *Liberty Co.,* Torreya St. Pk., 4M, 2F, 15 September 1979 (NCSM A2874) and several other males and females taken from March-October from 1968-1977 by various collectors (NCSM, FSCA, WAS) TYPE LOCALITY.

GEORGIA: *Early Co.,* Kolomoki Mounds St. Pk., 2M, 19 November 1977 (NCSM A1783) and M, 1 May 1983 (NCSM A4023). *Decatur Co.,* 1.4 mi. W Climax, 2M, F, 7 September 1959, L. Hubricht (RLH). *Camden Co.,* Crooked River St. Pk., 3M, 8F, 3 July 1977 (A1605) and M, 2 October 1980 (NCSM A3590). *Chatham Co.,* 1.7 mi. E Silk Hope, 2M, 12 September 1959, L. Hubright (RLH).

SOUTH CAROLINA: *Hampton Co.,* 0.8 mi. SE Hampton, M, 19 September 1959, L. Hubricht (RLH). *Beaufort Co.,* 2.5 mi. W. Bluffton, along SC hwy. 46, M, 12 September 1980 (NCSM A3507). *Jasper Co.,* 7 mi. S Hardeeville, M, 19 September 1959, L. Hubricht (RLH); and Ridgeland, M, 28 March 1975, D. Brody (AMNH).

Remarks. — Sigmoria (Cheiropus) australis has been reported twice before (Shelley 1979a, 1984a), first as representing an undiagnosed apherloriine genus and secondly as an undescribed species of *Hubroria.* I once thought *australis* related to species in the Cumberland Plateau of Tennessee for which the name *Hubroria* is available. Since the medial flange is broadest distad and the distal zone curves laterad from the peak, *australis* does conform in these traits to the Cumberland species. I therefore have spent days searching for *Sigmorias* from Jackson and Marshall counties to Birmingham, and since these efforts were unproductive, I do not think that the Cumberland fauna occurs south of the Tennessee River. Except for the medial flanges there is little similarity between the gonopods of *australis* and those of any Cumberland species as there would be in the case of a direct relationship. Only after revising *Cheiropus* (Shelley 1984a) did the affinity of *australis* for *stibarophalla* become evident. The latter, in the eastern Blue Ridge Mountains of North Carolina, is some 200 miles northwest of the closest known locality of *australis* in South Carolina. The region between *stibarophalla* and *australis* is occupied by more divergent forms of *Cheiropus*. Like *stibarophalla, australis* has a short prefemoral process, a sharp apical curve forming an arc with very narrow diameter, a short distal zone that curves laterad from the peak, and a medial flange that arises at the anterior bend and terminates at the apical curve, obscuring the distal zone in medial view. The similarities between their gonopods is evident by comparing Figs. 71-72 with Figs. 25-26 in Shelley (1981a).

Of nearly equal interest to the relationship with the allopatric *stibarophalla* are the allopatric populations of *australis* (Fig. 68). The two Alabama areas may eventually be joined by further collecting, but I doubt that the middle one will ever be connected with the eastern. There is no anatomical divergence and the forms in all three areas vary within similar limits.

The *Divergens* Group

The *divergens* group was proposed by Shelley (1983a) for a single species, but it is now enlarged to accommodate two species in the eastern Blue Ridge Mountains of the Carolinas. The distal zones curve strongly laterad from the peak but maintain their identities as distinct acropodal regions. Details are presented in Shelley (1981a, 1983a).

Components. — *divergens* Chamberlin, *stibarophalla* Shelley

The *Haerens* Group

In this and the following group, the distal zone is indistinguishable as a separate acropodal region and is represented instead by a solenomerite that is best viewed in lateral perspective. In the *haerens* group, the structure is located terminally on the distal extremity of the peak, perpendicular to the acropodal axis in two species and coaxial in one. The three included species, previously placed in the genus *Prionogonus,* were discussed in detail by

Shelley (1982). They are united by a synapomorphy, the row of spurs along the basal zone.

Components. — *haerens* (Shelley), *divaricata* (Shelley), *thrinax* (Shelley).

The *Planca* Group

The *planca* group contains the southernmost species in *Sigmoria,* which were formerly the sole components of the genus *Cheiropus* (Shelley 1984a). Here the solenomerite occurs at different positions on the acropodite stem, but always proximal to the tip. The basal zones are unmodified. The acropodite of *agrestis* displays a sigmoid curvature, which is absent in the curvilinear species *planca* and *serrata.* The peak is also greatly enlarged and thickened in these three species and often possesses marginal dentations. The fourth species, *persica,* is highly modified with the solenomerite arising basally from the acropodite. Further details are available in Shelley (1984a).

Components. — *planca* (Loomis), *agrestis* (Loomis), *persica* (Hoffman), *serrata* (Shelley)

Additional Record. — *serrata* — GA, Camden Co., Cumberland Island, M, 5 July 1984 (NCSM A4223).

SIGMORIA (SIGIRIA) Chamberlin, new status

Sigiria Chamberlin, 1939:9. Chamberlin and Hoffman, 1958:48. Jeekel, 1971:287.

Type species. — *Sigiria scorpio* Chamberlin, 1939 [= *Sigmoria rubromarginata* (Bollman)], by original designation.

Diagnosis. — Paranota yellow, red or violet/purple, metaterga with concolorous stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture and inserting between 7th legs; prefemoral process moderate; acropodites thin and fragile to moderately thick and heavy, oriented normally on coxa with inner surface directed anteriomediad; basal zone without modifications; medial flange present, laminate, location varying from proximal portion of peak to distal zone, lateral flange usually present, variably laminate; distal zone variable but usually more or less coplanar with basal zone.

Remarks. — *Sigiria* is revived from synonymy under *Sigmoria* for a heterogeneous assemblage in the southern Appalachians with concolorous paranota and metatergal stripes. The acropodites are highly variable but tend to connect through a spectrum of intermediate forms. Two species groups are recognized partly on the basis of geography, and partly on color.

The *Rubromarginata* Group

The *rubromarginata* group includes forms previously in this group, the *nigrimontis* and *inornata* [=*simplex* (Shelley 1981a)] groups, plus a new species on the Blue Ridge escarpment of Virginia. All except the last have red paranota and red metatergal stripes, this species being yellow. The acropodites are highly variable, but the extremes tend to join through forms of *nigrimontis intermedia,* which is appropriately named. The species-group name of *simplex* (Shelley 1981a) is changed to avoid homonymy with *simplex* Shelley (1977), and the former eastern race of *rubromarginata,* which is continuous with intergrades on the Blue Ridge Front, is elevated to specific status. Its range is isolated from *rubromarginata* by around 30 miles, and anatomical divergence has occurred.

Components. — *rubromarginata* (Bollman); *austrimontis* Shelley; *whiteheadi,* new species; *nigrimontis n. nigrimontis* (Chamberlin), *n. intermedia* (Hoffman), *n. angulosa* Shelley, *n. unicoi* (Shelley); *inornata, new* name; *truncata* Shelley; *sigirioides* Shelley.

Sigmoria (Sigiria) austrimontis Shelley, new status

Sigmoria rubromarginata austrimontis Shelley, 1981a:102-103, Figs. 100-103.

Under this binomial I include the homogeneous population in the South Mountains of North Carolina and the contiguous, heterogeneous assemblage of forms anatomically intermediate between it and *rubromarginata* occurring in the Blue Ridge escarpment and western piedmont lowlands. Genetic interchange with *rubromarginata* is no longer possible, as the ranges are now disjunct, and as stated in the introduction, such populations are now recognized at the specific level. This situation is clearly one where a formerly continuous range, with localized gene pools in the peripheries and intergrade forms in an intermediate geographical position, underwent vicariance partitioning.

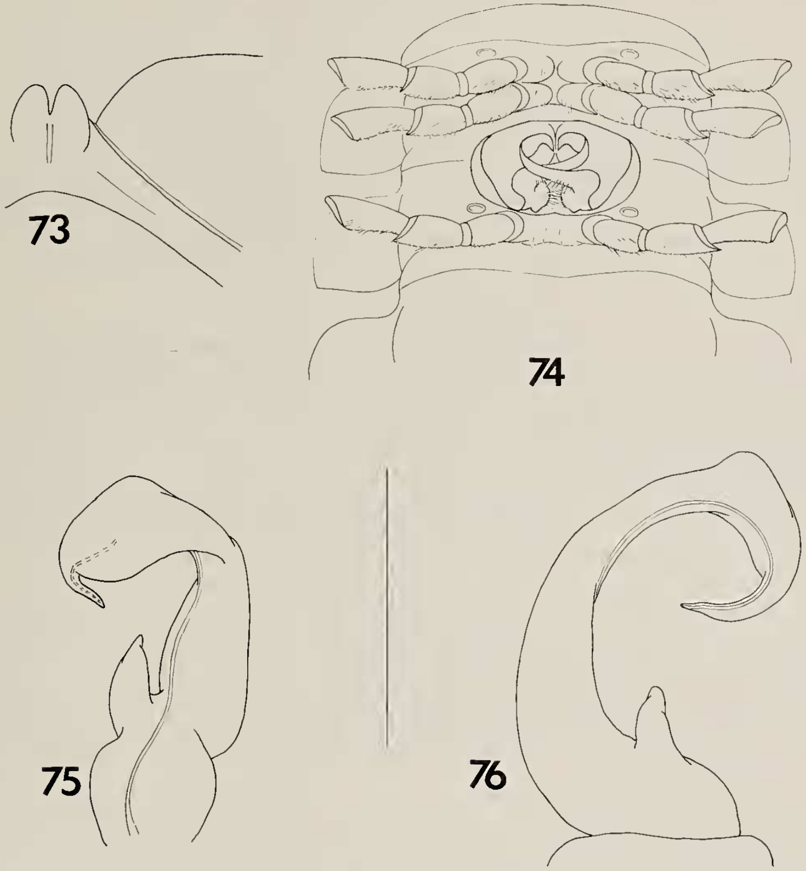
Sigmoria (Sigiria) whiteheadi Shelley, new species Figs. 73-76

Type specimens. — Male holotype and two female paratypes (RLH) collected by R.L. Hoffman, 20 May 1983, from Patrick Co., VA, along Laurel Creek on Blue Ridge parkway at mile 174.3. Male paratype (RLH) taken by same collector at same locality, 23 June 1984.

Diagnosis. — A small species of *Sigmoria* with medial flange on peak and with yellow paranota and yellow metatergal stripes; gonopods with following diagnostic characters: prefemoral process short, blunt;

acropodite moderately thick and heavy, curvature forming narrow arc; peak short and gently curved; distal zone curving laterad from peak, not coplanar with basal zone, bent sharply inward into arch at midlength; medial flange thin and narrow, margin linear, poorly demarcated from acropodite stem; lateral flange located opposite medial, flared outward proximad.

Color in Life. — Paranota bright lemon yellow; metaterga black with concolorous yellow stripes along caudal margins connecting paranotal markings; collum with yellow stripes along both anterior and posterior edges.



FIGS. 73-76. *Sigmoria (Sigiria) whiteheadi.* 73, process of 4th sternum of holotype, caudal view. 74, gonopods *in situ,* ventral view of holotype. 75, telopodite of left gonopod of the same, medial view. 76, the same, lateral view. Scale line for fig. 74 = 1.00 mm; line for other figs. = 1.00 mm for 73 and 76; 1.25 mm for 75.

Holotype. — Length 31.1 mm, maximum width 6.9 mm, W/L ratio 22.2%, depth/width ratio 62.3%. Segmental widths as follows:

collum 5.1 mm
2nd 6.1
3rd 6.5
4th 6.7
5th-14th 6.9
15th 6.5
16th 6.2
17th 5.5
18th 4.4

Somatic features similar to those of *I. latior,* with following exceptions:

Width across genal apices 3.7 mm, interantennal isthmus 1.1 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>4=6>5>1>7. Genae with trace of central impressions. Facial setae as follows: epicranial 2-2, interantennal absent, frontal 1-1, genal 3-3, clypeal about 8-8, labral about 14-14.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, ends broadly rounded and extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 9, blunt on 10-15, and more acute caudally. Peritremata relatively flat, faintly elevated above paranotal surface. Ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum small, divided, much shorter than widths of adjacent coxae (Fig. 73); 5th sternum with low paramedian knobs between 4th legs and flattened, elevated areas between 5th, both much shorter than widths of adjacent coxae; 6th sternum with slight recession between caudal legs to accommodate apical curvatures of acropodites. Postgonopodal sterna elevated above stricture, flattened, with bicruciform impressions on 8-9 and variably broad, shallow central depressions thereafter. Coxae without tubercles; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 2.6 mm wide and 1.4 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 74) with acropodites projecting anteriomediad from aperture, overlapping in midline and curving dorsad over opposite side, extending only slightly beyond anterior margin. Gonopod structure as follows (Figs. 75-76): Prefemoral process short, blunt, directed toward peak. Acropodite moderately thick and heavy, well sclerotized, tightly curved forming narrow arch, overhanging and extending well beyond level of prefemoral process; basal zone relatively long, widest basally; anterior bend sharp, well defined; peak short and gently curved; apical curve broad, poorly defined; distal zone moderately long, curving slightly laterad from peak and not coplanar with basal zone, bent abruptly (90°) inward into center of arch at midlength or termination point of flanges, relatively straight distal to bend with sides narrowing smoothly and continuously to acuminate tip; latter directed toward basal zone. Medial flange thin and narrow, arising imperceptibly on proximal part of peak but terminating clearly at midlength of distal zone, margin curving distad. Lateral flange larger than and located opposite medial, arising on distal extremity of peak, terminating at midlength of distal zone, flared outward proximad, margin linear thereafter. Prostatic groove crossing to lateral surface at anterior bend, continuing to terminal opening.

Female paratype. — Length 31.8 mm, maximum width 7.7 mm, W/L ratio 24.2%, depth/width ratio 65.0%. Cyphopods *in situ* with corners of receptacles visible in apertures, valves directed dorsolaterad. Receptacle large, cupped over ventral corners of valves, surface rugulose. Valves moderate in size, subequal, surfaces finely granulate.

Male paratype. — The male paratype agrees with the holotype in all details.

Ecology. — Dr. Hoffman discovered the type specimens in rhododendron litter in a rhododendron/red maple woods. Since this spot is along a creek, *whiteheadi* seems to be a cove species. It is only the second one found in rhododendron leaves, the other being *truncata* (Shelley 1981a). Others occur near rhododendron, but always in litter of associated hardwood species, usually red maple or dogwood. A male of *l. latior (Sigmoria)* was collected only a foot or so from the male paratype.

Distribution. — Known only from the type locality.

Remarks. — The closest collection of the *rubromarginata* group to *whiteheadi* is Morganton, North Carolina, approximately 120 miles SSW, where *austrimontis* occurs. The acropodite of *whiteheadi* is thicker and heavier than that of *austrimontis,* but in both the distal zones are twisted approximately 90° mediad revealing the faces of the medial and lateral flanges in medial view. However, the apical curve is narrower than in *austrimontis,* forming an arc of shorter diameter, and the distal zone distal to the flanges curves more strongly into the acropodite arch. Thus, the distal half of the distal zone, which is longer than in *austrimontis,* is partly obscured in medial view by the flanges. The prefemoral process is also longer than in *austrimontis* and is not bifurcate.

Sigmoria (Sigiria) inornata Shelley, new name

Sigmoria simplex Shelley, 1981a:45-49, Figs. 29-34.

Sigmoria (Sigiria) inornata is proposed as a new name for this species to avert homonymy resulting from the inclusion of *Croatania* in *Sigmoria* and the resultant transferral of *C. simplex* Shelley, 1977. Priority for the species-group name is with the transferred species.

The *Stenogon* Group

As presently conceived, the *stenogon* group is markedly different in composition from that in its original proposal (Shelley 1981a). One species, *nantahalae (Falloria),* is now in another subgenus, and two species have been added that were previously in the *latior* and *nigrimontis* groups. the gonopods of the three species of the *stenogon* group appear dissimilar in medial view, but considerable conformity is apparent in lateral perspective (compare Figs. 22, 60, and 130 in Shelley (1981a)). The color varies from yellow in the north through red in the central part of the group's range to purple or violet in the south.

Components. — *stenogon* Chamberlin, *areolata* Shelley, *disjuncta* Shelley.

SIGMORIA (FALLORIA) Hoffman, new status

Falloria Hoffman, 1948:93-94. Chamberlin and Hoffman, 1958:33. Jeekel, 1971:264. Hoffman, 1979:159.
Hubroria Keeton, 1960:42. Hoffman, 1979:159. **NEW SYNONYMY.**

Type species. — Of *Falloria, Apheloria bidens* Causey, 1942, by original designation; of *Hubroria, H. picapa* Keeton, 1960, by original designation.

Diagnosis. — Paranota usually red, occasionally white or light yellow, metaterga with contrasting stripes, usually blue, connecting paranotal markings except when latter white or light yellow; gonopods *in situ* with acropodites extending well beyond anterior margin or aperture and inserting between 7th legs; prefemoral process highly variable, deeply or apically divided, long and basally globose or moderate or short; acropodites usually moderately thick and heavy, oriented normally on coxa with inner surface directed anteriomediad or with inner surface directed mediad; basal zone usually without modifications, occasionally with dense tubercles; medial flange usually present and laminate, location varying from basal to distal zones; lateral flange present or absent, variably laminate; distal zone variable, either coplanar with basal zone or directed strongly laterad and nearly coplanar with peak.

Remarks. — *Falloria* is revived from synonymy under *Sigmoria* as the oldest available name for the heterogeneous assemblage with largely contrasting paranotal and metatergal colors in the western part of the generic range. The acropodites are highly variable, and eight species groups are recognized.

The *Nantahalae* Group

The *nantahalae* group contains only the single species, which is unique to the subgenus in the red/white coloration, the absence of a medial flange, and the presence of a tooth. Further details are available in accounts by Hoffman (1958a) and Shelley (1981a).

Component. — *nantahalae* Hoffman.

The *Leucostriata* Group

The *leucostriata* group is characterized by a greatly reduced medial flange on the proximal part of the peak, small medial and lateral lobes opposing each other proximally on the distal zone, and a curved or bent distal zone which extends into the arch. It consists of two allopatric species in the western fringe of the Blue Ridge Province in Tennessee and north Georgia. One, *leucostriata,* is the only member of the subgenus with concolorous paranota/metaterga; the other, *xerophylla,* exhibits the typical red/blue pattern.

Components. — *leucostriata* Shelley, *xerophylla* Shelley.

The *Bidens* Group

Previously, the *bidens* group was monobasic, but I now add an undescribed species with a contiguous range to the north. It has been known for years, but thinking that it might be referrable to *Hubroria,* I withheld description until the validity of this name could be assessed. Whereas *bidens* has a long, narrow medial flange on the proximal part of the peak and a separate subconical tooth distal to the flange (Shelley 1981a), the new species lacks a tooth and its short medial flange has a broad variable lobe, arises distally on the peak, and terminates on the proximal part of the distal zone. Its affinity for *bidens* is demonstrated by the prefemoral processes. That of *bidens* is basally globose, while that of the new species is variable and moderately globose in the most proximal population. The *bidens* group occurs in the Sevier County, Tennessee, portion of the GSMNP, from Elkmont to Greenbrier.

Components. — *bidens* (Causey), *prolata,* new species.

Sigmoria (Falloria) prolata Shelley, new species Figs. 77-83

Type specimens. — Male holotype (NCSM A1939) and 4 male and 7 female paratypes collected by R.M. Shelley and W.B. Jones, 19 May 1978, in the Ramsey Cascade Parking Area, Greenbrier Section, GSMNP, Sevier Co., TN. Male and female paratypes deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* with red paranota and blue transverse metatergal stripes; gonopods with following diagnostic characters: prefemoral process long, configuration variable, widest basally, tapering distad, extending beyond level of tip of acropodite; latter moderately thick and heavy, arch broadly curved and overhanging prefemoral process; basal zone continuous with peak and distal zone through broad, poorly defined anterior bend and apical curve; distal zone variable but generally moderately long, directed laterad from peak, not coplanar with basal zone, bent abruptly inward into arch at midlength in medial view; tip elongate and acuminate or reflexed; medial and lateral flanges short, opposing each other on distal zone and distal extremity of peak, with variable lobes.

Color in Life. — Paranota red; metaterga black with wide, blue stripes along caudal edges connecting paranotal markings; collum with blue stripes along both anterior and posterior edges.

Holotype. — Length 41.1 mm, maximum width 9.7 mm, W/L ratio 23.6%, depth/width ratio 58.8%. Segmental widths as follows:

collum 7.8 mm	14th 9.4
2nd 8.6	15th 9.0
3rd 9.1	16th 8.5
4th 9.4	17th 7.3
5th-13th 9.7	18th 5.7

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 1.7 mm. Antennae extending back to caudal edges of 3rd paranota, relative lengths of antennomeres 2>3>6>5>4>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 10-10, labral 16-16.

Dorsum smooth, polished, with only faint wrinkling on anterior half of paranota. Collum broad, ends produced slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on 7-13, becoming progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum small, apically divided, much shorter than widths of adjacent coxae (Fig. 77); knobs between anterior legs of 5th sternum minute, lower than broad elevated areas between posterior legs; 6th sternum convexly recessed between 7th legs to accommodate apical curvature regions of acropodites. Postgonopodal sterna flat and plate-like, with bicruciform impressions on segments 8-9 and variably broad, shallow, central impressions on remaining segments. Coxae with low, blunt tubercles beginning on segment 8, becoming sharply acute on 10-15 and lowly rounded on remaining segments; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.0 mm, wide and 1.9 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface and thickened. Gonopods *in situ* (Fig. 78, of paratype) with acropodites overlapping near midlengths in midline of aperture, extending forward beyond anterior margin with distal zones crossing. Gonopod structure as follows (Figs. 79-80): Prefemoral process long, extending beyond level of tip of acropodite, widest basally, tapering smoothly and continuously to acuminate tip, latter curved gently anteriad, directed toward apical curve. Acropodite moderately thick, a broad, continuous curve with indistinguishable regions overhanging and extending well beyond level of prefemoral process; peak and basal zone continuous through anterior bend and continuous with distal zone through apical curve; distal zone moderately long, curving laterad and not coplanar with basal

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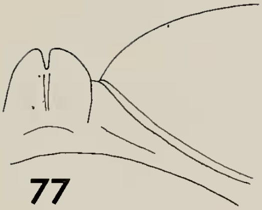
Figs. 77-83. *Sigmoria (Falloria) prolata.* 77, process of 4th sternum of holotype, caudal view. 78, gonopods *in situ,* ventral view of paratype. 79, telopodite of left gonopod of holotype, medial view. 80, the same, lateral view. 81, telopodite of left gonopod of male from Porter Creek parking area, medial view. 82, distal part of acropodite of the same, lateral view. 83, telopodite of left gonopod of male from Roaring Fork Nature Trail, medial view. Scale line for fig. 78 = 1.00 mm; line for other figs. = 1.00 mm for 79-83, 1.33 mm for 77.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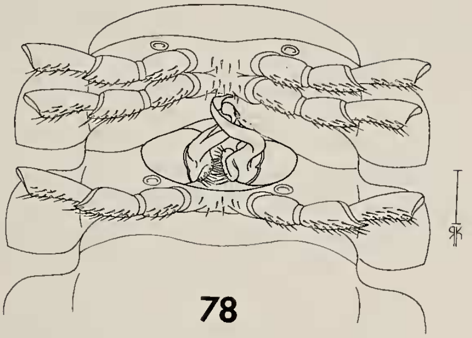
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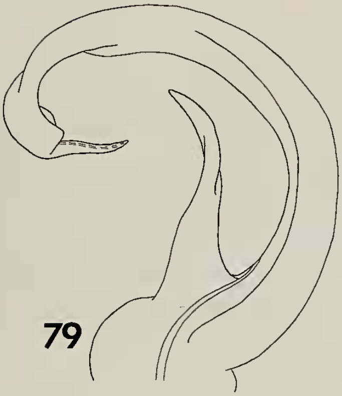
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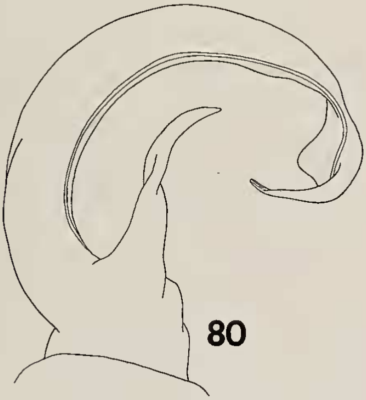
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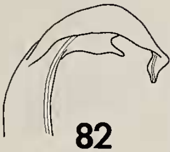
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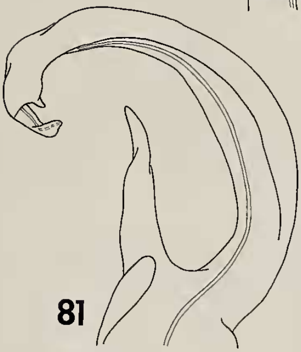
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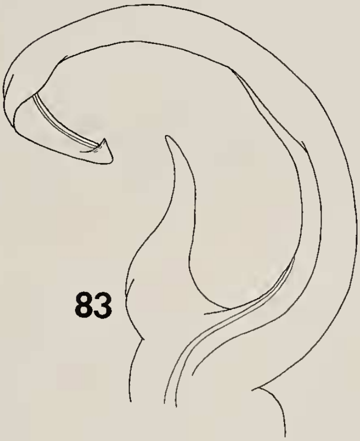
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zone, bent abruptly inward into arch at midlength and tapering smoothly and continuously to acuminate tip; latter directed toward distal curve of prefemoral process; medial flange located opposite lateral flange, arising on distal extremity of peak, terminating in broad, triangular lobe at midlength of distal zone. Lateral flange arising at apical curve, terminating at midlength of distal zone, margin gently rounded. Prostatic groove crossing to lateral side on basal zone, continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 42.8 mm, maximum width 10.4 mm, W/L ratio 24.3%, depth/width ratio 68.3%. Cyphopods *in situ* with corner of receptacles visible in apertures, valves directed caudolaterad. Receptable very large, completely enveloping valves, with ridges and lobes, surface rugulose. Valves small, subequal, surfaces finely granulate.

Variation. — Considerable variation is evident in both the prefemoral process and acropodite of *prolata.* All samples from the Greenbrier section of the GSMNP differ from the types, which are from the northernmost point reachable by road in this area. Those from Porter Creek parking area (NCSM A3007), the southernmost point in Greenbrier, have a more linear prefemoral process, a shorter distal zone with a reflexed tip, and a short distal projection on the medial flange (Figs. 81-82). Males collected along Rhododendron Creek on the entrance road to Greenbrier (NCSM A1942) resemble those from Porter Creek except the medial flange is trapezoidal and lacks the projection. The male collected along Roaring Fork Nature Trail (NCSM A1895), about 4 miles south of Greenbrier, displays a broadly linear medial flange that is not rounded, a narrow and inconspicuous lateral flange, a long distal zone, a reflexed tip, and a prefemoral process that is moderately globose basally and similar to that in contiguous populations of *bidens* (Fig. 83). Thus specimens from the geographic extremes, Ramsey Cascade and Roaring Fork, exhibit long distal zones, but only those from the former have reflexed tips. There are also north-south geographic trends toward a narrower medial flange and a basally broader prefemoral process, which grades into the globose condition found in *bidens* (see Shelley 1981a, Figs. 80-81, p. 82).

Ecology. — *Sigmoria (F.) prolata* is a cove inhabiting species.

Distribution. — Known only from the Greenbrier and Roaring Fork sections of the GSMNP near Gatlinburg in Sevier County, Tennessee. I have searched in vain for *prolata* along TN highway 73, which runs along the western edge of the Park in Tennessee and connects these two sections, and thus believe it to be restricted to these secluded areas of the Park. The species is abundant in Greenbrier and can be easily collected in May or June. It is comparatively rare in Roaring Fork, however, as two subsequent trips to the site of the first collection failed to produce more individuals. Specimens were examined as follows:

TENNESSEE: *Sevier Co.,* Greenbrier Section, GSMNP, 8.2 mi. ENE Gatlinburg, Ramsey Cascade pkg. area, 5M, 7F, 19 May 1978 (NCSM A1939) TYPE LOCALITY; 7.5 mi. ENE

Gatlinburg, Porter Creek pkg. area, 9M, 5F, 8 May 1980 (NCSM A3007); 4.0 mi. ENE Gatlinburg, along Greenbrier entrance rd. 1.8 mi. E jct. TN hwy. 73, 2M, 3F, 19 May 1978 (NCSM A1942); and unknown sites in Greenbrier, M, 14 June 1939, D.H. Lowrie, and M, 15 June 1942, C.H. Seevers (both RLH). Roaring Fork Nature Trail between 3rd and 4th bridges, 2.9 mi. ESE Gatlinburg, M, F, 16 May 1978 (NCSM A1895).

Remarks. — Sigmoria (F.) prolata links forms in the GSMNP, which are clearly referrable to *Sigmoria s. lat.,* with those in the Cumberland Plateau with laterally directed distal zones that could be assigned to *Hubroria.* Hence, this species is a major reason why the latter name is placed in synonymy.

The *Tuberosa* Group

The single species of this group is characterized by a number of apomorphic traits including hirsute postgonopodal sterna, a circular gonopodal aperture, tubercles on the outer surface of the basal zone of the acropodite, fusion of the tooth and medial flange, an additional flange on the inner surface of the distal zone, and a unique, complex tip. The species is known only from the eastern part of the GSMNP and adjacent areas in Swain County, North Carolina.

Component. — tuberosa Shelley.

The *Aphelorioides* Group

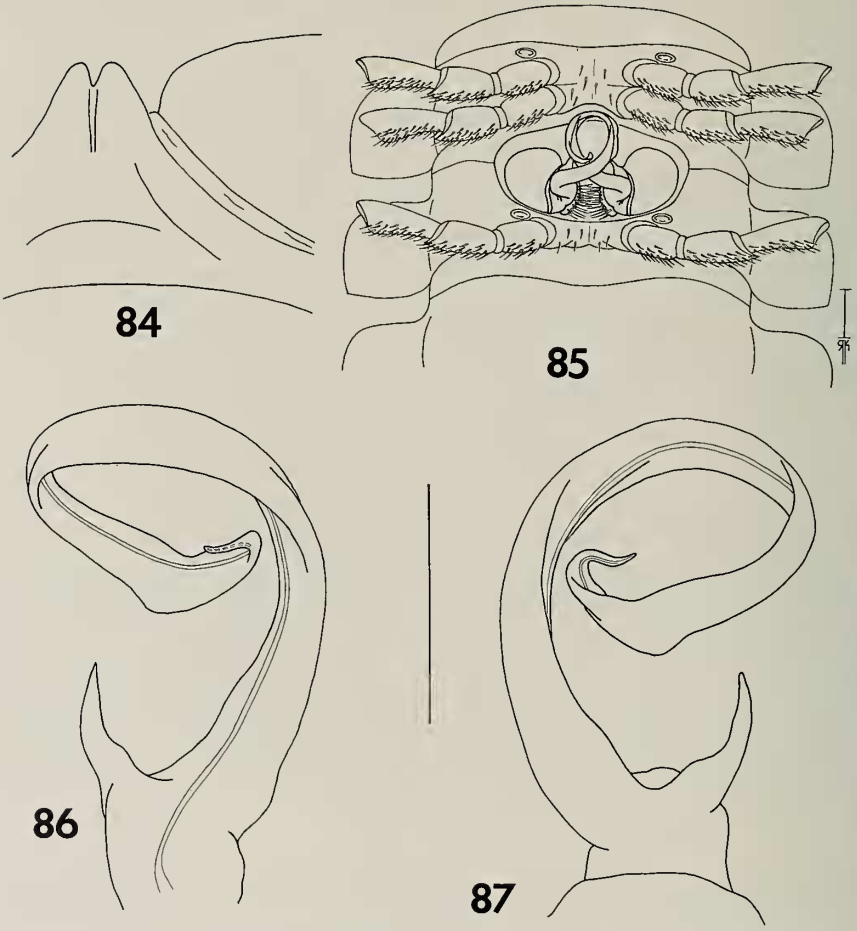
A single species group is proposed for *aphelorioides.* The general configuration of the prefemoral process is shared with *xerophylla* and *nantahalae,* and the circular acropodite is similar to that of *ainsliei;* however, there are important differences in the two loops as discussed in the species accounts. The *aphelorioides* group occurs between *xerophylla* and the *translineata* group in the Great Smoky Mountains south of the National Park. As with the latter, it spans the state line, occurring in the western fringe of North Carolina.

Components. — aphelorioides, new species.

Sigmoria (Falloria) aphelorioides Shelley, new species Figs. 84-87

Type specimens. — Male holotype (NCSM A2468) and 3 male and 2 female paratypes collected by R.M. Shelley and W.B. Jones, 12 October 1978, from Monroe Co., TN, 17.3 mi. SE Madisonville, along TN highway 165, 0.5 mi W Bald River Falls, Cherokee National Forest. Three male paratypes (A2466) taken by same collectors on same date, 14.3 mi SE Madisonville, along TN highway 165 at Tellico Ranger Station, Cherokee National Forest. Two male and one female paratypes (RLH) collected by L. Hubricht, 12 June 1953, from Monroe Co., 1.5 mi. E Tellico Plains, Tellico River Gorge. Male and female paratypes deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* without medial acropodal flange, with red paranota and blue transverse metatergal stripes, gonopods



FIGS. 84-87. *Sigmoria (Falloria) aphelorioides.* 84, process of 4th sternum of holotype, caudal view. 85, gonopods *in situ,* ventral view of paratype. 86, telopodite of left gonopod of holotype, medial view. 87, the same, lateral view. Scale line for fig. 85 = 1.00 mm; line for other figs. = 1.00 mm for 84; 1.14 mm for 86-87.

with following diagnostic characters: acropodites *in situ* usually lying over and under one another; prefemoral process relatively long, upright, acuminate; acropodite moderately thick and heavy, slightly overhanging prefemoral process, configuration circular, anterior bend and apical curve broad but well defined, distal zone not coplanar with basal zone, extending laterad from peak, curving down behind arch of acropodite and extending nearly to level of basal zone, expanded proximal to tip, latter acuminate, bent abruptly dorsad.

Color in Life. — Paranota red; metaterga black with wide, blue transverse stripes along caudal edges connecting paranotal spots; collum with blue stripes along both anterior and caudal edges.

Holotype. — Length 42.4 mm, maximum width 10.7 mm, W/L ratio 25.2%, depth/width ratio 61.7%. Segmental widths as follows:

collum	7.0 mm	14th	10.5
2nd	8.9	15th	10.2
3rd	9.6	16th	9.9
4th-8th	10.4	17th	8.7
9th-13th	10.7	18th	6.1

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.8 mm, interantennal isthmus 1.9 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres 2 > 3 > 4 = 5 = 6 > 1 > 7. Genae with slight central impressions. Facial setae as follows: epicranial 1-1, interantennal and frontal absent, genal 2-2, clypeal about 15-15, labral about 18-18, merging with clypeal series and continuing for short distance along genal border, 2 setae per side.

Terga relatively coriaceous in middorsum, more so on paranota. Collum broad, ends extending well beyond those of following tergite. Paranota moderately depressed, angled ventrad and continuing slope of dorsum; caudolateral corners rounded on segments 1-4, becoming blunt and progressively more acute thereafter. Peritremata distinct, sharply elevated above metazonal surface; ozopores located in swelling just caudal to midlength, directed dorsolaterad.

Process of 4th sternum (Fig. 84) deeply divided apically, length subequal to widths of adjacent coxae; 5th sternum with small paramedial knobs between 4th legs and larger knobs between 5th legs; both shorter than widths of adjacent coxae; 6th sternum convexly recessed between 7th legs to accommodate curvature of acropodites. Postgonopodal sterna relatively flat and plate-like, with shallow central impressions, becoming deeper caudally. Coxal tubercles beginning on 10th legs, becoming longer and sharper posteriorly; prefemoral spines arising on segment 5, becoming progressively more acute caudally.

Gonopodal aperture broadly ovoid, 4.4 mm long and 1.9 mm wide at midpoint, indented anteriolaterad, sides strongly elevated above metazonal surface. Gonopods *in situ* (Fig. 95, of paratype) with acropodites lying over and under each other in midline of aperture, not intertwining, peaks extending forward just beyond anterior margin of aperture. Gonopod structure as follows (Figs. 86-87): Prefemur moderate in size, with relatively long, upright, acuminate prefemoral process arising on anterior side, bent slightly at midlength, with suggestion of tooth basally. Acropodite relatively thick and heavy, well sclerotized, circumscribing nearly complete circle of considerably more than one vertical plane, extending slightly beyond outer level of prefemoral process. Basal zone long, without modifications; anterior bend broad, well defined; peak gently curved and rounded, highest at midlength, leaning slightly mediad and essentially coplanar with basal zone; apical curve relatively broad; distal zone long, extending laterad from peak and not coplanar with basal zone, expanding markedly near midlength then narrowing rapidly to acuminate tip; recurved and slightly bisinuate. Prostatic groove crossing to lateral side at anterior bend, running along inner surface of distal zone to opening at tip.

Male paratypes. — The prefemoral process is uncinate on a few paratypes, and the expansion of the distal zone is much broader in the males from Tellico Gorge.

Female paratype. — Length 42.7 mm, maximum width 10.7 mm, W/L ratio 25.1%, depth/width ratio 81.3%. Cyphopods *in situ* with side of receptacle visible in aperture, valves directed dorsad. Receptacle large, cupped over ventral surfaces of valves, surface rugulose. Valves relatively small, subequal, surfaces finely granulate.

Variation. — Neither size nor color pattern varies appreciably in *aphelorioides.* The most notable gonopodal variation involves the midlength expansion on the distal zone, which is broadest in the center of the range (Monroe Co.) and reduced in the eastern and western peripheries. The expansion is barely detectable in the male from North Carolina and resembles the condition in *ainsliei.* In the paratypes from Tellico Gorge and the male from McMinn County, the tip is broader and not as recurved as in other specimens (reflexed in the latter), and the distal part of the distal zone is "scoop-shaped."

Ecology. — *Sigmoria (F.) aphelorioides* inhabits moist rhododendron coves.

Distribution. — A small area in the Blue Ridge Province south of the Little Tennessee and north of the Hiwassee Rivers, lying just north of the area of *xerophylla.* In Tennessee the species in known only from the Cherokee National Forest, and it occurs in the Tellico Wildlife Management area in eastern Monroe County. The range extends across the North Carolina state line into the western fringe of Swain County, and *aphelorioides* should be expected in the Joyce Kilmer-Slickrock Wilderness Area of Graham County. Specimens were examined as follows:

TENNESSEE. *Monroe Co.,* 8.8 mi E Madisonville, along unnumbered rd. off co. rd. 2568, M, 3F, 13 October 1978 (NCSM A2475); 14.3 mi SSE Madisonville, along TN hwy. 165 at Tellico Ranger Station, 3M, 12 October 1978 (NCSM A2466); 17.3 mi SSE Madisonville, along TN hwy. 16, 0.5 mi W Bald River Falls, 4M, 2F, 12 October 1978 (NCSM A2468) TYPE LOCALITY; and 1.5 mi. E Tellico Plains, Tellico Gorge, 2M, F, 12 June 1953. L. Hubricht (RLH). *McMinn Co.,* 11.2 mi. SE Athens, along co. rd. 4371, 0.5 km W jct co. rd. 4276, M, F, 13 October 1978 (NCSM A2479).

NORTH CAROLINA: *Swain Co.,* 0.3 mi N Tapoco (in Graham Co.), along trail off US hwy. 129 just inside Graham Co. line, M, 26 June 1974 (NCSM 2460).

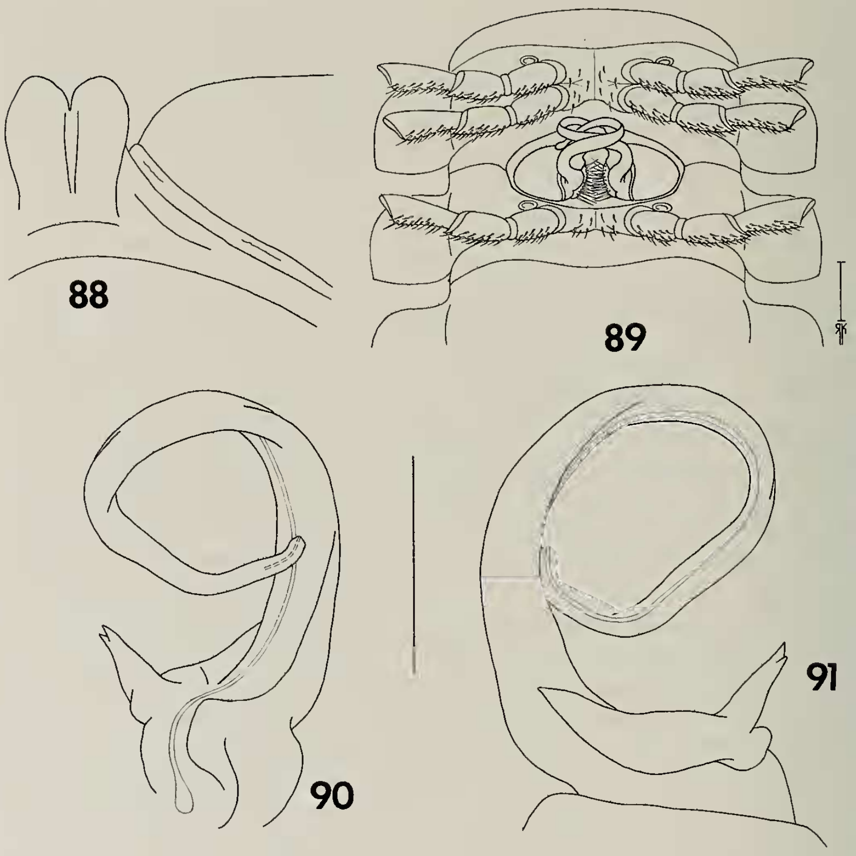
Remarks. — Though phenotypically similar to *ainsliei* in having a circular acropodite, *aphelorioides* differs in that the loop passes through considerably more than one vertical plane. In *aphelorioides* the distal zone curves laterad from the peak, whereas it is not coplanar with the basal zone in *ainsliei.* These looped or circular configurations are convergent with the condition in *Apheloria,* hence *aphelorioides'* specific name; they are also convergent with that in *trimaculata (Rudiloria).* The distal zone is not broader at midlength in *ainsliei,* but most males of *aphelorioides* display a distinct expansion, particularly those from the center of the distribution. This expansion is in about the same position on the distal zone as the lobes in *trimaculata kleinpeteri (Rudiloria).* Thus, in the Great Smoky Mountains and from Virginia to Canada there are forms with circular acropodites that possess and lack an expansion on the distal zone. Their relative statuses, however, differ; those in the Smokies are reproductively isolated, whereas the others connect through intergrades and represent geographic races. In addition to the acropodal differences, the distinct prefemoral processes of *ainsliei* and *aphelorioides* also indicate reproductive isolation. In contrast, the projections of *t. trimaculata* and *t. kleinpeteri (Rudiloria)* are nearly identical.

The *Translineata* Group

Four species, two newly described, are added to the *translineata* group, bringing its composition to seven species, four in the Great Smoky Mountains area of Tennessee and North Carolina and three in the Cumberland Plateau of Tennessee. One species, *ainsliei,* occurs in the former and extends west into the fringe of the adjacent Ridge and Valley Province. The species are united by a divided prefemoral process; *translineata, lyrea, ainsliei,* and *forficata* have large, deeply divided structures, but it is shorter, and the division more shallow, in *fumimontis.* The processes are large and cupped, and the division subapical in *houstoni* and *abbreviata.* In *translineata, lyrea,* and *fumimontis* the peak is tilted laterad, and the medial flanges are long and narrow, arising on the anterior bend and terminating near the beginning of the apical curve. The first two also display a rounded lobe on the lateral edge of the acropodite near the beginning of the apical curve. The acropodal configurations vary, with *translineata* and *fumimontis* having flattened peaks and short distal zones, while *ainsliei* has a circular acropodite that forms a complete loop. *Sigmoria (F.) lyrea* exhibits an intermediate configuration but does not occupy an intermediate geographical position. In the Blue Ridge forms the distal and basal zones are coplanar, but the former curves strongly laterad in the Cumberland species and is nearly coplanar with the peak in *houstoni.* At first glance, *ainsliei* does not appear congeneric, as its circular acropodite is convergent with those in *Apheloria* (it was originally assigned to this genus by Chamberlin (1921)), and it also lacks acropodal adornments, most notably a medial flange.

Despite these differences, the divided prefemoral process of *ainsliei* is clearly indicative of shared ancestry with other members of the *translineata* group.

Components. — *translineata* Shelley; *lyrea* Shelley; *fumimontis* Shelley; *ainsliei* (Chamberlin); *forficata,* new species; *houstoni* Chamberlin; *abbreviata,* new species.



Figs. 88-91. *Sigmoria (Falloria) ainsliei.* 88, process of 4th sternum of holotype, caudal view. 89, gonopods *in situ,* ventral view of male from Sevier Co., TN. 90, telopodite of left gonopod of holotype, medial view. 91, the same, lateral view. Scale line for fig. 89 = 1.00 mm; line for other figs. = 1.00 mm for 88 and 91; 1.33 mm for 90.

Sigmoria (Falloria) ainsliei (Chamberlin), new combination Figs. 88-91

Apheloria ainsliei Chamberlin, 1921:232, Fig. 1. Attems, 1938:168, Fig. 184. Chamberlin and Hoffman, 1958:18.

Type specimen. — Male holotype (MCZ) collected by George G. Ainslie on unknown date from unspecified locality in Knox Co., TN.

Diagnosis. — A large species of *Sigmoria* without medial acropodal flange, usually with red paranota and blue transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: acropodites interlocking and intertwined; prefemoral process large, divided basally into two unequal components, lateral component longer and directed laterad behind base of acropodite, medial component upright and directed ventrad; acropodite moderately thick and heavy, slightly overhanging prefemoral process, configuration circular, anterior bend and apical curve broad but well defined, distal zone coplanar with basal zone, extending into arch and overlapping latter; tip narrowing on both sides to blunt, central termination.

Color in Life. — Paranota usually red, occasionally blue, metaterga with blue stripes along caudal margins.

Holotype. — Length 52.0 mm, maximum width 12.5 mm, W/L ratio 24.0%, depth/width ratio 68.0%. Segmental widths as follows:

collum	9.0 mm	13th	12.3
2nd	10.4	14th	12.0
3rd	10.9	15th	11.5
4th	11.6	16th	10.6
5th-7th	12.0	17th	9.3
8th-12th	12.5	18th	6.4

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 2.0 mm. Antennae reaching back to middle of 3rd paranota, relative lengths of antennomeres 2 > 3 > 4 = 5 > 6 > 1 > 7. Genae with slight central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, clypeal about 12-12, labral about 16-16.

Terga smooth, polished, moderately coriaceous on paranota. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, angled ventrad and continuing slope of dorsum, caudolateral corners rounded through segment 5, blunt on 6-13, becoming progressively more acute posteriorly. Peritremata relatively flat, not sharply elevated above paranotal surface. Ozopores located in swellings near middle of paranota, opening dorsolaterad.

Process of 4th sternum (Fig. 88) moderate, subequal to widths of adjacent coxae; 5th sternum with large paramedial knobs between both leg pairs, shorter than widths of adjacent coxae; 6th sternum convexly recessed between both leg pairs to accommodate apical curvatures of acropodites. Postgonopodal sterna relatively flat and plate-like, with large, shallow central impressions on caudal segments and transverse grooves between leg pairs on all segments. Small coxal tubercles present on legs of segments 9-16; prefemoral spines beginning on legs of segment 6, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 5.4 mm wide and 2.4 mm long at midpoint, indented anteriolaterad, sides raised above metazonal surface. Gonopods *in situ* (Fig. 89, not this specimen) with acropodites projecting ventrad from aperture, bending sharply mediad and overlapping and intertwining in midline, peaks extending forward beyond anterior edge of aperture and inserting in depression between 7th legs, apices directed ventrad on respective sides of aperture. Gonopod structure as follows (Figs. 90-91): Prefemur large, subglobose, with basally divided prefemoral process arising on anterior side, components of process diverging by more than 90°; lateral component longer than medial, directed laterad and extending behind base of acropodite, tip blunt, obscured in medial view; medial component apically bifurcate and upright, directed ventrad. Acropodite moderately thick and heavy, circumscribing complete circle of slightly more than one vertical plane, extending only to outer level of prefemoral process. Basal zone long, without modifications; anterior bend broad, well defined; peak gently curved and rounded, highest at midlength, leaning mediad and overhanging prefemur, not coplanar with basal zone; apical curve relatively broad but well defined; distal zone long, curving broadly into arch and overlapping basal zone, thus forming complete circle with peak and distal extremity of basal zone, essentially coplanar with peak, bent slightly at midlength and again just proximal to tip; latter blunt, directed subventrad, only slightly discontinuous with distal zone. Medial and lateral flanges absent. Prostatic groove crossing to lateral side of acropodite at anterior bend and continuing to opening in center of tip.

Description of Female. — Based on specimen from 16.3 km E Maryville, Blount County, TN (NCSM A2460).

Length 55.5 mm, maximum width 12.4 mm, W/L ratio 22.3%, depth/width ratio 78.2%. Cyphopods *in situ* with edge of receptacle visible in aperture, valves directed dorsolaterad. Receptacle large, globose, located entirely on medial sides of valves, surfaces rugulose. Valves moderate and subequal in size, diverging dorsad, surfaces finely granulate.

Variation. — *Sigmoria (F.) ainsliei* varies considerably in size, with some individuals dramatically larger than others. Dimensions of the male and a female from 10.2 miles east of Maryville (NCSM A2460) were 56.1 mm in length and 12.8 mm in width, and 59.8 mm in length and 13.3 mm in width, respectively. On the gonopods the prefemoral process is highly variable. Males from Knox County possess a simple, two-pronged structure, as described for the holotype, but most individuals from Blount and Sevier counties have one or two additional spurs on the ventral surface arising near the juncture of the two components. The configuration of the acropodite is reasonably constant, but the distal zone is slightly bisinuate in a few males and widens distally (proximal to the bend at the tip) in ones from the southern part of the range.

Ecology. — In the Blue Ridge Province in and near the GSMNP, *ainsliei* inhabits the moist rhododendron coves typical of *Sigmoria s. lat.* However, these environments are rare in the more western Ridge and Valley Province, particularly in the valley between the Smokies and Knoxville. Here I have found *ainsliei* in several predominantly hardwood habitats under leaves near water, but sample A2460 was taken under thick layers of leaves on a steep bank.

Distribution. — A small area in the adjacent fringes of the Ridge and Valley and Blue Ridge Provinces, ranging from just north of the French Broad River on the University of Tennessee campus in Knoxville to Tennessee Highway 73 (Little River Road) in the GSMNP. The species does not penetrate far into the GSMNP and has not been encountered east of Highway 73, for example along the road to Cades Cove. However, *ainsliei* is common in the Park near the Sinks, Metcalf Bottoms Picnic Area, and Little Greenbrier School, as well as in adjacent areas outside the park near Townsend and Wear Valley. It should be expected in western Sevier County and in the corner of Loudon County near Friendsville, although these areas contain so much cleared land that suitable milliped habitat is rare. Specimens were examined as follows:

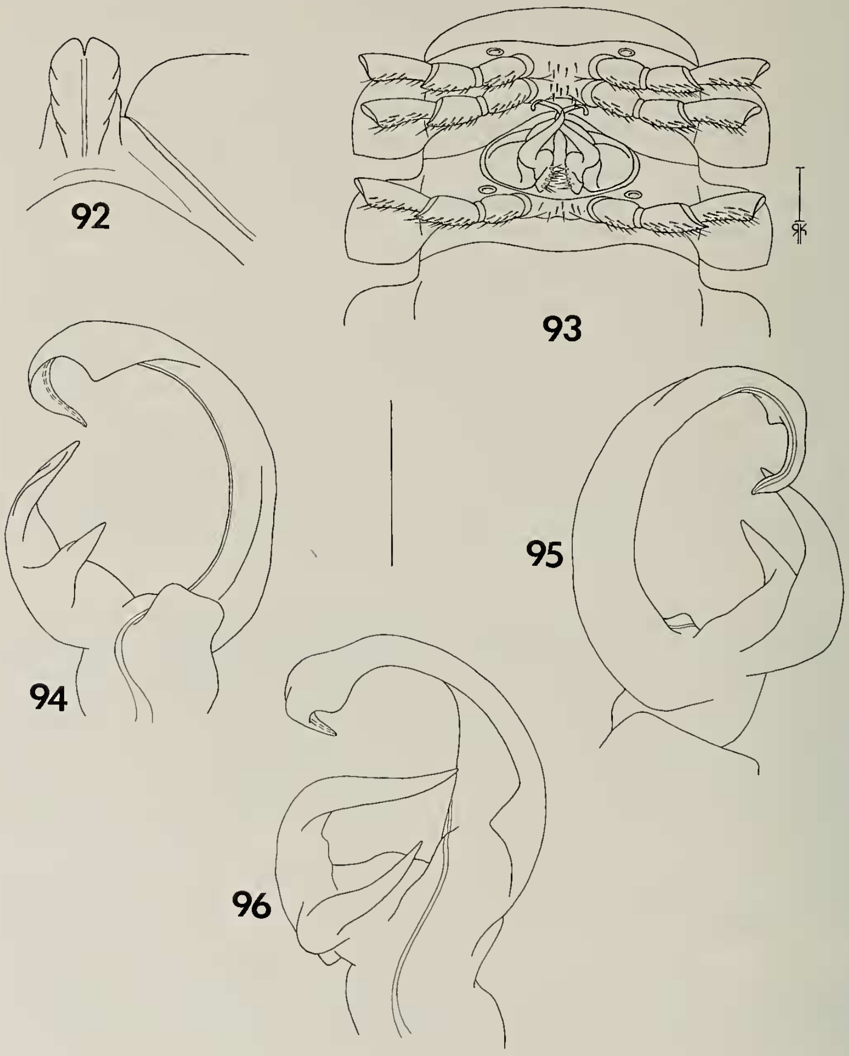
TENNESSEE: *Knox Co.,* locality and date unspecified, M, G.G. Ainslie (MCZ) TYPE SPECIMEN; Knoxville, Cherokee Bluff, 2M, 17 May 1951, L. Hubricht (RLH) and University of Tennessee campus, M, 18 April 1972, W. Tolbert (RLH). *Blount Co.,* 10.2 mi E Maryville, along unnumbered rd., 1.0 km N jct. co. rd. 2427, M, 2F, 11 October 1978 (NCSM A2460); 6.4 me SE Maryville, along unnumbered rd., 3.2 km N jct. Foothills Parkway, F, 11, October 1978 (NCSM A2462); 3.4 mi N Townsend along co. rd. 2422, M, 9 April 1981 (NCSM A3659); and GSMNP, along TN hwy. 73 at crossing of Little R., M, F, 17 May 1978 (NCSM A1932). *Sevier Co.,* 1.4 mi. W Gatlinburg, along Norton Creek Rd. off US Hwy. 441, 3M, F, 8 May 1980 (NCSM A3015); Little Greenbrier School, GSMNP, 5M, 6F, 17 May 1978 (NCSM A1935); and GSMNP, along TN hwy 73, 0.6 mi N Metcalf Bottoms Picnic Area, 2M, F, 9 August 1981, R.M. Shelley and H. Enghoff (NCSM A3723).

Remarks. — Sigmoria (F.) ainsliei lacks a medial flange, but a new medial edge arising at the anterior bend is suggestive of a flange. This is actually caused by torsion. The medial surface of the basal zone shifts to the lateral side at the anterior bend, and a new medial edge arises at this point, extends the length of the peak, and terminates at the apical curve, whereupon a third medial edge arises. The acropodite is not broader through the peak, at it would be with a flange, and tapers into the distal zone.

Sigmoria (Falloria) forficata Shelley, new species Figs. 92-96

Type specimens. — Male holotype (NCSM A2630) and two male and two female paratypes collected by R.M. Shelley and R.K. Tardell, 7 May 1979, 4.2 mi. SE Crab Orchard, along Fall Creek near Ozone Twp., Cumberland Co., TN. Male and female paratypes deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* with medial flange extending between proximal parts of peak and distal zone and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process massive, usually divided basally into two long components, medial one shorter and usually more linear, lateral one longer and curved broadly anteriad; acropodite relatively thin, arch broadly curved



Figs. 92-96. *Sigmoria (Falloria) forficata.* 92, process of 4th sternum of holotype, caudal view. 93, gonopods *in situ,* ventral view of paratype. 94, telopodite of left gonopod of holotype, medial view. 95, the same, lateral view. 96, telopodite of left gonopod of male from Scott Co., TN, medial view. Scale line for fig. 93 = 1.00 mm; line for other figs. = 1.00 mm for each.

and extending over prefemoral process; basal zone gently curved, with or without a basomedial projection; anterior bend and apical curve poorly defined; distal zone moderately long, directed laterad from peak and not coplanar with other sections, curving into arch distad and tapering to acuminate tip; medial flange variable but with broadly triangular lobe on distal extremity of peak; lateral flange inconspicuous, a small lobe on distal zone opposite distal extremity of medial flange.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal edges connecting paranotal markings; collum with blue stripes along both anterior and posterior margin.

Holotype. — Length 48.8 mm, maximum width 11.3 mm, W/L ratio 23.2%, depth/width ratio 58.4%. Segmental widths as follows:

collum	6.8 mm	14th	10.8
2nd	8.5	15th	9.8
3rd	9.9	16th	9.5
4th	10.3	17th	8.4
5th-6th	10.8	18th	6.3
7th-13th	11.3		

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 1.7 mm. Antennae relatively long, reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>6>4=5>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 12-12, labral about 16-16.

Dorsum smooth, polished, and moderately coriaceous, especially on anterior halves of paranota. Collum broad, ends extending well below those of following tergite. Paranota strongly depressed, angling sharply downward and exceeding slope of dorsum, caudolateral corners rounded through segment 7, blunt on 8-13, and becoming progressively more acute posteriorly. Peritremata relatively flat and indistinguishable, ozopores located near middle of peritremata, opening dorsolaterad.

Sternum of segment 4 with long, apically divided process, longer than widths of adjacent coxae (Fig. 92); that of segment 5 with long apically divided process between anterior legs and two medially coalesced knobs between 5th legs, projections nearly equal in length to each other and to widths of adjacent coxae; 6th sternum deeply and convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna as follows: those of segments 8-10 with flattened elevated areas and blunt caudally directed lobes subtending anterior and posterior coxae, respectively, these strongest on segment 8 and progressively less pronounced on 9-10; remaining sterna without elevations between anterior legs and with progressively smaller ones between posterior legs, becoming progressively more plate-like posteriorly with variably broad central impressions. Coxae with blunt tubercles beginning on caudal legs of segment 9, sharply acute on 11-14, diminishing thereafter; prefemoral spines on segment 5, becoming progressively longer and more acute posteriorly.

Gonopodal aperture ovoid, 4.6 mm wide and 2.6 mm long at midpoint, strongly indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 93, of paratype) with acropodites angling mediad and overlapping in midline of aperture, then curving laterad and extending slightly beyond anterior margin; prefemoral processes with components crisscrossing. Gonopod structure as follows (Figs. 94-95): Prefemoral process massive, divided basally into two components, a short, straight medial one, and a longer, broadly curved anterior one, both directed toward basal zone and tapering smoothly and continuously to acuminate tips. Acropodite rather thin, forming broadly curved arch, extending nearly to level of distal extremity of prefemoral process; basal zone gently curved, continuous with peak through anterior bend; latter broad, poorly defined; peak gently curved, apex near midlength; apical curve broad, poorly defined; distal zone moderately long, curving laterad from peak and not coplanar with basal zone or peak, curving inward distally and tapering to acuminate tip; latter directed toward basal zone. Medial flange large and conspicuous, broadly triangular, arising on proximal part of peak, terminating on proximal part of distal zone. Lateral flange small and inconspicuous, a broadly rounded lobe opposite distal half of medial flange. Prostatic groove crossing to lateral side on peak and continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 47.0 mm, maximum width 11.3 mm, W/L ratio 24.0%, depth/width ratio 69.9%. Cyphopods *in situ* with corners of receptacles partly visible in aperture, partially obscured by large, convoluted cyphopodal membranes, valves directed caudad. Receptable moderately large, completely enveloping valves, with lobes and ridges, surface rugulose. Valves small, subequal, surfaces finely granulate.

Variation. — The sternal projections are similar to those of the holotype in all males except those from Hamilton County, where they are smaller. In this individual the process on segment 4 is equal in length to the widths of the adjacent coxae; the anterior projection on segment 5 is absent; and there are broad, separate, elevated areas between the posterior legs that are much shorter than the adjacent coxal widths. The postgonopodal sternal lobes on segments 8-10 are also smaller.

On the gonopods, the males from Cumberland County agree closely with the holotype, although that from 8.5 miles E of Crab Orchard (NCSM A2766) has a small triangular projection from the medial edge of the basal zone near midlength. The male from Scott County, the northernmost locality, has a more rounded medial flange that arises proximally on the basal zone and has a distinct spine from the proximomedial edge (Fig. 96). The latter closely resembles the condition in *arcuata (Cleptoria)* in piedmont South Carolina. The Morgan County male has a broad prefemoral process that is cupped on the ventral surface and not as deeply divided, so the medial projection appears more as a basal spur than a separate structure. The medial flange in the Morgan County male is less expanded and terminates more abruptly on the distal zone. South of Cumberland County, the Bledsoe County male is nearly identical to the holotype, but in those from Hamilton County, the medial component of the prefemoral process is longer and curved toward the other, which in turn is narrower and more sinuous than in the holotype.

Ecology. — *Sigmoria (F.) forficata* is a cove inhabiting species.

Distribution. — The Cumberland Plateau of Tennessee. *Sigmoria (F.) forficata* occurs sporadically across the width of Tennessee from near the Kentucky to near the Georgia/Alabama borders. It may eventually be discovered in McCreary County, Kentucky, but the Tennessee River marks its southern range limit, as extensive searches south of the waterway in Marion and Hamilton counties, and adjacent parts of Georgia and Alabama, have been unsuccessful. Specimens were examined as follows:

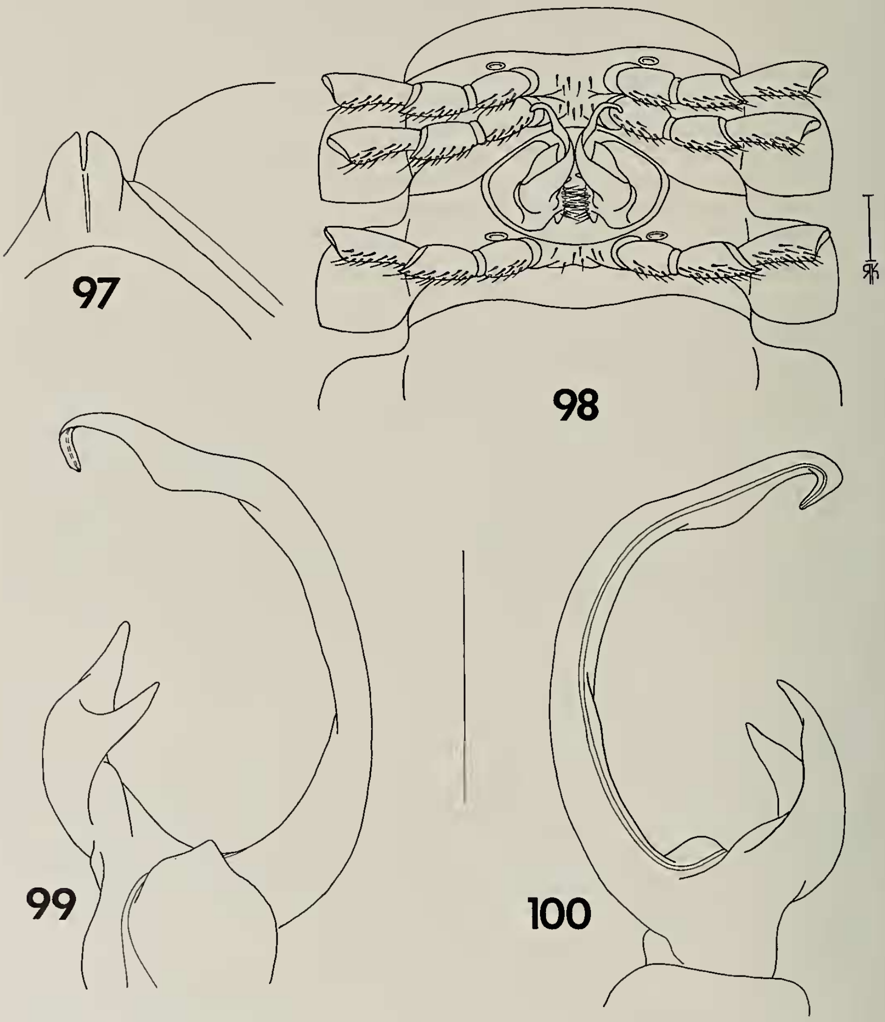
TENNESSEE. — *Scott Co.,* 7.0 mi. S. Huntsville, along co. rd. 2342 near Brimstone Cr., M, F, 8 June 1979 (NCSM A2724). *Morgan Co.,* 4.3 mi. SW Wartburg, along Emory R. on edge of Catoosa Wildlife Man. Area, M, 2F, 7 June 1979 (NCSM A2718). *Cumberland Co.,* 8.5 mi. N Crossville, along Fox Cr. in Catoosa Wildlife Man. Area, M, 2F, 15 June 1979 (NCSM A2765); 4.2 mi. SE Crab Orchard, along Falls Cr. near Ozone, 3M, 2F, 7 May 1979 (NCSM A2630) TYPE LOCALITY; and 8.5 mi. E Crab Orchard, along co. rd. 4382, 2.2 mi. W jct. co. rd. 2590, M, 2F, 15 June 1979 (NCSM A2766). *Bledsoe Co.,* 2.8 mi. SE Pikeville, along TN hwy. 30, M, F, 25 May 1983 (NCSM A4137). *Hamilton Co.,* Signal Mountain, M, F, 18 August 1956, R.L. Hoffman (RLH); and Rainbow Lake Wilderness Area nr. Signal Mountain, M, 22 May 1983 (NCSM A4113).

Remarks. — Some traits of *forficata* are convergent with ones found in congeners in piedmont South Carolina, many miles east across the Appalachians. The large, convoluted cyphopodal membrane is similar to that in *catawba, saluda,* and *simplex (Croatania);* and the long process on the 4th sternum closely resembles those in these species plus *shelfordi* and *arcuata (Cleptoria).* The distinct basal spine on the medial flange in the Scott County male also resembles those in these species as does the slightly distal triangular lobe in a Cumberland County male. Lastly, the prefemoral process is massive in *forficata, catawba,* and *saluda,* and the curvature of the lateral component is similar to that of the entire structure in *catawba* and *saluda* (compare Figs. 30 and 32 with Figs. 1, 3, 7, and 8 in Shelley 1977).

Sigmoria (Falloria) abbreviata Shelley, new species Figs. 97-100

Type specimens. — Male holotype (A4136) and one male and three female paratypes collected by R.M. Shelley, 24 May 1983, from Fall Creek Falls State Park, Van Buren Co., TN. Additional paratypes collected in same locality as follows: two females by same collector, 17 June 1976; and one male and four females by R.M. Shelley and R.K. Tardell, 13 May 1979. Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on distal extremity of peak and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process large, ventral surface convex distad, divided at midlength into two subequal, diverging components; acropodite thin and fragile, arc broadly curved and extending over but not beyond level of prefemoral process; basal zone broadly curved; anterior bend and apical curve poorly defined; peak and distal zone relatively short; latter curving sublaterad from former, not coplanar with other sections, bent into arch distad and tapering to acuminate tip; medial flange a small, rounded lobe; lateral flange narrow



Figs. 97-100. *Sigmoria (Falloria) abbreviata.* 97, process of 4th sternum of holotype, caudal view. 98, gonopods *in situ,* ventral view of paratype. 99, telopodite of left gonopod of holotype, medial view. 100, the same, lateral view. Scale line for fig. 98 = 1.00 mm; line for other figs. = 1.00 mm for 99-100; 1.33 mm for 97.

and inconspicuous, represented by a slightly wider acropodite stem opposite medial flange.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal margins connecting paranotal spots; collum with blue stripes along both anterior and posterior edges.

Holotype. — Length 37.0 mm, maximum width 9.1 mm, W/L ratio 24.6%, depth/width ratio 60.4%. Segmental widths as follows:

collum	6.9 mm	15th	8.9
2nd	7.2	16th	8.7
3rd	7.9	17th	7.5
4th	8.8	18th	5.4
5th-14th	9.1		

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.4 mm, interantennal isthmus 1.4 mm. Antennae reaching back to middle of 3rd paranota, relative lengths of antennomeres 2>3>5>6=4>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 16-16, labral 22-22.

Dorsum smooth, polished, moderately coriaceous. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on 7-13, becoming progressively more acute caudally. Peritremata thick and conspicuous, strongly elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum moderately long, equal to widths of adjacent coxae (Fig. 97); 5th sternum with two paramedian knobs between anterior legs, shorter than widths of adjacent coxae, and broad, flattened, elevated areas between posterior legs; 6th sternum convexly recessed between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on 8-9, becoming progressively flatter and more plate-like posteriorly with variably broad, shallow, central impressions. Coxae with blunt tubercles beginning on segment 10, becoming progressively more acute posteriorly; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 3.4 mm wide and 1.7 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 98, of paratype) with acropodites angling toward midline, either touching or overlapping near midlengths, then curving anteriolaterad and extending beyond anterior margin. Gonopod structure as follows (Figs. 99-100): Prefemoral process large, curving slightly ventrad at midlength and convex distally on ventral surface, divided into two diverging, subequal, acuminate components, directed toward midlength of acropodite. Acropodite moderately thin, forming broadly curved arc, overhanging prefemoral process; basal zone broadly curved, continuous with peak through anterior bend; latter broad, poorly defined; peak moderately long; apical curve broad, poorly defined; distal zone relatively short, curving sublaterad from peak and not coplanar with other sections, bending inward into arch distad and tapering to blunt tip. Medial flange small, margin smoothly rounded, located on distal extremity of peak. Lateral flange barely detectable, a slightly wider spot in stem of acropodite opposite medial flange. Prostatic groove crossing to lateral side on basal zone, continuing to terminal opening.

Male Paratypes. — The only variation in the male paratypes involves the shape and relative lengths of the projections of the prefemoral process.

Female Paratype. — Length 39.6 mm, maximum width 9.9 mm, W/L ratio 25.0% depth/width ratio 59.6%. Cyphopods *in situ* with corners of receptacles protruding through folded, convoluted membranes in aperture, valves directed caudomediad. Receptacle large, located along anterior sides of valves, with ridges and lobes, surface rugulose. Valves moderate, subequal, surfaces finely granulate.

Variation. — The Bledsoe County male agrees with the holotype.

Ecology. — *Sigmoria (F.) abbreviata* is a cove inhabiting species.

Distribution. — Known only from the central Cumberland Plateau. Specimens were examined as follows:

TENNESSEE. — Van Buren Co: Fall Creek Falls St. Pk., 2F, 17 June 1976 (NCSM A888), M, 4F, 13 May 1979 (NCSM A2693), and 2M, 3F, 24 May 1983 (NCSM A4136) TYPE LOCALITY. *Bledsoe Co.,* 22 mi. E Spencer, along TN hwy 30, 0.5 mi. E jct. TN hwy. 101, M, 2F, 14 May 1979 (NCSM A2697).

Remarks. — I have collected *abbreviata* two places in Fall Creek Falls State Park. The sample with the holotype came from behind the park office; the others were taken along the trails behind the nature center.

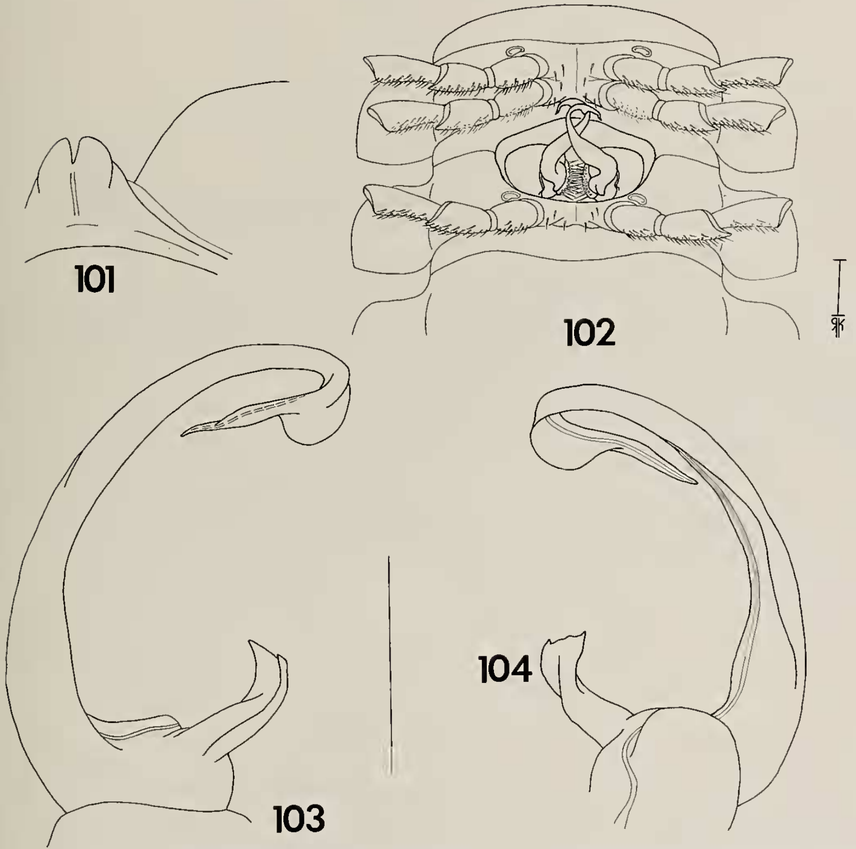
Although it has a bifurcate prefemoral process, *abbreviata* shares more features with *houstoni* than with *forficata.* The bifurcation is more of an elaboration on the squared/cupped condition found in *houstoni,* as the corners are elongated and the margin between them depressed, than it is true bifurcation, in which separate projections arise from a common base. The affinity between *abbreviata* and *houstoni* is also seen in the acropodites, as the medial flanges are in the same general locations, and the distal zones have the same general curvatures. The flange and distal zone are shorter (abbreviated) in *abbreviata,* hence the specific name. These is no indication of a flange on the basal zone in *abbreviata* as in some variants of *forficata,* and *abbreviata* also lacks the sternal modifications of the latter. Perhaps *abbreviata* and *houstoni* were once joined by intergrade forms that have disappeared leaving two isolated populations. Both warrant specific recognition because of these differences.

Sigmoria (Falloria) houstoni Chamberlin Figs. 101-104

Sigmoria houstoni Chamberlin, 1943:144, Fig. 1. Hoffman, 1950:5. Chamberlin and Hoffman, 1958:50.

Type specimens. — Male holotype and female allotype (RVC); locality, date, and collector unknown. The vial label and the three prior references give Houston, Harris County, Texas, as the type locality, but this is clearly the result of a sampling mixup. As shown in Fig. 151, no member of the tribe Apheloriini occurs within 250 miles of Houston. The type locality should be somewhere in Franklin, Grundy, or Marion counties, Tennessee, the only places where *houstoni* has been authentically taken. The date of collection and the collector reported by these authors may also be wrong. Because of this confusion, the following description is of a male collected from Marion County, along TN highway 108, 5.8 mi S of the Grundy County line.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange extending between midlengths of basal and distal zones and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process moderately long, ventral surface convex distad, apical margin with corners produced, with or without additional spurs; acropodite



FIGS. 101-104. *Sigmoria (Falloria) houstoni.* 101, process of 4th sternum of male from Marion Co., TN, caudal view. 102, gonopods *in situ,* ventral view of the same. 103, telopodite of left gonopod of the same, submedial view. 104, the same, lateral view. Scale line for fig. 102 = 1.00 mm; line for other figs. = 1.00 for 101 and 104; 1.14 mm for 103.

relatively thin, curving broadly over but not beyond distal extremity of prefemoral process; basal zone gently curved; anterior bend poorly defined; peak short, continuing overall curvature of acropodite; apical curve well defined; distal zone relatively long, directed laterad and coplanar with peak, tapering distally to acuminate tip; medial flange long and narrow, expanded into rounded terminal lobe on proximal part of distal zone; lateral flange absent.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal edges connecting paranotal markings; collum with blue stripes along both margins.

Description. — Length 37.1 mm, maximum width 8.9 mm, W/L ratio 24.0%, depth/width ratio 48.3%. Segmental widths as follows:

collum	5.8 mm	14th	8.4
2nd	6.9	15th	8.1
3rd-4th	7.9	16th	7.5
5th-7th	8.7	17th	6.5
8th-13th	8.9	18th	5.0

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.3 mm. Antennae relatively short, extending only to caudal edge of 2nd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 10-10, labral 12-12.

Dorsum smooth, moderately coriaceous in midline. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 4, blunt in midbody region, becoming progressively more acute caudally. Peritremata distinct, strongly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with small lobe between 3rd legs, much shorter than widths of adjacent coxae (Fig. 101); that of segment 5 with low knobs between 4th legs, much shorter than widths of adjacent coxae, and low flattened areas between 5th legs; sternum of segment 6 convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna smooth and flat, bicruciately impressed on segments 8-10, with variably broad, shallow, central impressions on remaining segments. Coxae with blunt tubercles beginning on segment 5, sharp and distinct on all legs.

Gonopodal aperture elliptical, 2.9 mm wide and 1.6 mm long at midpoint, indented slightly anteriolaterad, sides raised above metazonal surface. Gonopods *in situ* (Fig. 102) with acropodites angling mediad and overlapping in midline of aperture, curving laterad, overlapping again, and projecting slightly beyond anterior margin. Gonopod structure as follows (Figs. 103-104): Prefemoral process moderately large, rectangular, narrowest basally, convex ventrally, distal corners curved ventrad and directed toward basal zone. Acropodite thin and laminate, forming broadly curved, open arc, extending over but not beyond level of distal extremity of prefemoral process; basal zone gently curved, continuous through anterior bend with peak; anterior bend broad, poorly defined; peak continuing general curvature of basal zone and anterior bend; apical curve short, well defined; distal zone moderately long, curving directly laterad and coplanar with peak, tapering smoothly and continuously to acuminate tip, latter slightly bisinuous. Medial flange long, arising proximally on basal zone, continuing through peak as linear lamina, expanding into rounded lobe on proximal part of distal zone, terminating abruptly at distal extremity of lobe near midlength of distal zone. Lateral flange absent. Prostatic groove crossing from medial to lateral sides around proximal part of peak, continuing to terminal opening.

Description of Female from Grundy Co. — Length 42.8 mm, maximum width 10.6 mm, W/L ratio 24.8%, depth/width ratio 69.8%. Cyphopods *in situ* with corners of receptacles protruding through folded, convoluted membranes in aperture, valves directed caudomediad. Receptacle large, located along anterior sides of valves, with ridges and lobes, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — The gonopods of *houstoni* are rather uniform. Some prefemoral processes are more elaborate than others and have short terminal and subterminal spurs, but this is random variation with no geographic component. Similarly, the medial flange widens slightly basally then narrows again at the approximate location of the anterior bend in some males.

Ecology. — The specimens of *houstoni* I collected came from dry, open, hardwood litter well removed from water. It therefore is not a cove species and has different ecological preferences from *forficata* and the Appalachian congeners.

Distribution. — Cumberland Plateau of Grundy, Marion, and Franklin counties, Tennessee. It should also be expected in the western fringe of Sequatchie County. Specimens were examined as follows:

TENNESSEE. — *Grundy Co.*, 4 mi. N Palmer, along co. rd. 4350, 23 May 1983 (NCSM A4122); 2.5 mi. S Palmer, along TN hwy. 108, 0.3 mi. N Marion co. line, M, 2F, 12 May 1979 (NCSM A2684); and Grundy St. For. near Tracy City, 2M, 2F, 26 April 1979 (A2606). *Marion Co.*, 11.1 mi. N Whitwell, along TN hwy. 108, 1.8 mi. S Grundy co. line, M, 26, April 1979, A.L. Braswell, R.E. Ashton, and R. Franz (NCSM A2589); 5.8 mi. S Grundy co. line, along TN hwy. 108, 3M, 3F, 12 May 1979 (NCSM A2685) and 3.5 mi. N Whitwell, along TN hwy. 108, 0.9 mi. S. jct. co. rd. 4303, 2M, 23 May 1983 (NCSM A4121). *Franklin Co.*, Sewanee, 2M, date unknown, S. Lazell (FSCA).

Remarks. — Because the distal zone curves directly laterad and thus is coplanar with the peak, the acropodite was tilted slightly ventrad in figure 103 to show this section.

The *Picapa* Group

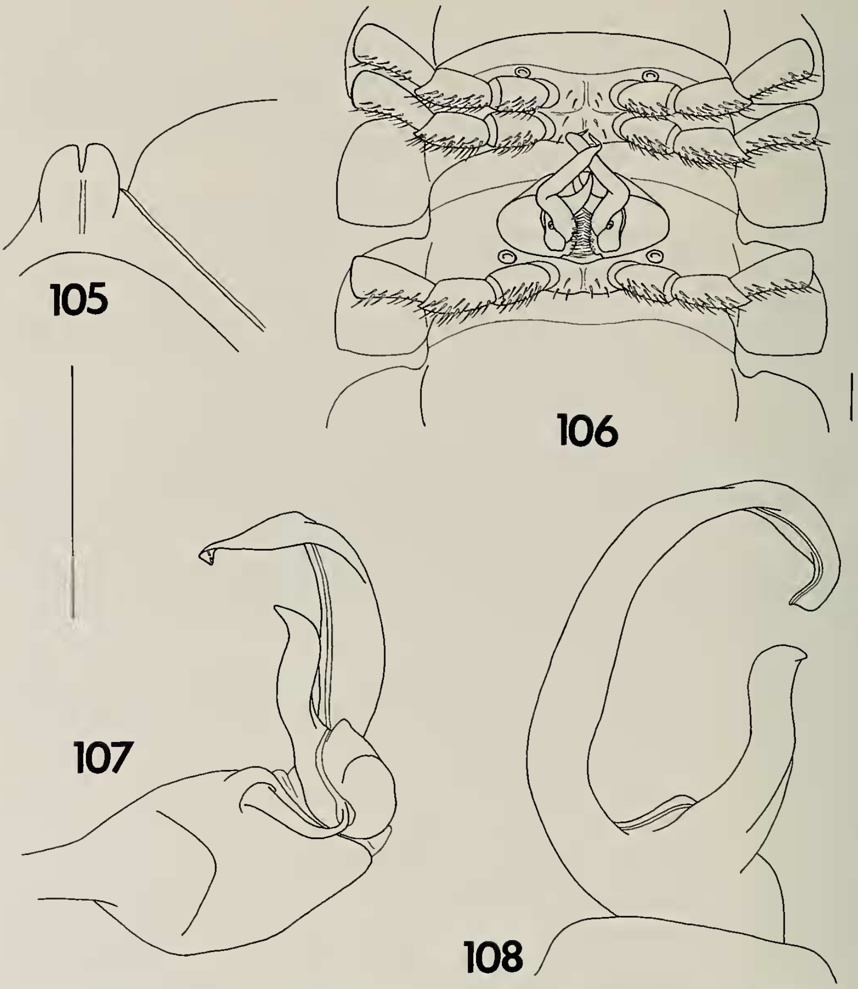
A single species group is proposed for *picapa*, which differs from the other Cumberland species in the large, bisinuate, undivided prefemoral process. The laterally directed distal zone is not reflective of a separate genus as Keeton (1960) thought when he described it. The species is not a cove inhabitant and is known only from a small area in northern Morgan County, Tennessee.

Component. — *picapa* (Keeton).

Sigmoria (Falloria) picapa (Keeton), new combination Figs. 105-108

Hubroria picapa Keeton, 1960:2-4, Figs. 1-4.

Type specimens. — One male and two female paratypes (FMNH) collected by B. Benesh, June 1949, at Sunbright, Morgan Co., TN. Male



Figs. 105-108. *Sigmoria (Falloria) picapa.* 105, process of 4th sternum of paratype, caudal view. 106, gonopods *in situ,* ventral view of topotype. 107, left gonopod of paratype, medial view. 108, telopodite of the same, lateral view. Scale line for fig. 106 = 1.00 mm; line for other figs. = 1.00 mm for 108; 1.33 mm for 105; 1.78 mm for 107.

paratype (RLH) taken by same collector, 2 June 1952, at Burrville, Morgan County. One male and one female topotypes (NCSM A3363) collected by R.M. Shelley and M.S. Morgan, 22 July 1980, from Morgan Co., 2.3 mi. NNE Sunbright, along US hwy. 27, 0.5 mi. N jct. co. rd. 2438. The male holotype apparently is missing from the NMNH, where Keeton (1960) reported its deposition. Two loan requests to this institution failed to produce it, and its location is unknown.

Diagnosis. — A large species of *Sigmoria* with medial flange running between distal extremities of basal zone and peak and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process long, widest basally, tapering distad, bisinuately curved; acropodite moderately thick and heavy, arch an inverted L, extending to level of prefemoral process; basal zone long, gently curved; anterior bend well defined; peak flattened, angling slightly downward, narrowing distad; apical curve poorly defined; distal zone short, directed laterad and coplanar with peak, obscured by latter in medial view, narrowing distad and expanding into blunt tip; medial flange broadest distad; lateral flange located on peak opposite medial flange.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal margins connecting paranotal markings; collum with red and blue stripes along anterior and posterior edges, respectively.

Male Paratype from Sunbright. — Length 42.9 mm, maximum width 10.4 mm, W/L ratio 24.2%, depth/width ratio 60.6%. Segmental widths as follows:

collum	7.5 mm	14th	10.2
2nd	8.7	15th	9.7
3rd	9.6	16th	8.9
4th-7th	10.0	17th	7.8
8th-13th	10.4	18th	6.0

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.1 mm, interantennal isthmus 1.9 mm. Antennae reaching back to caudal edge of 3rd paranota; relative lengths of antennomeres 2> 3> 6> 5> 4> 1> 7. Genae with flat central impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 12-12, labral about 16-16.

Dorsum smooth, polished, moderately coriaceous on paranota. Collum broad, ends extending slightly beyond those of adjacent tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on 7-11, becoming progressively more acute caudally. Peritremata thick and distinct, sharply elevated above paranota, ozopores located near middle of peritremata, opening dorsolaterad.

Process of 4th sternum apically divided, shorter than widths of adjacent coxae (Fig. 105); knobs of 5th sternum coalesced medially into ventrally directed process, shorter than widths of adjacent coxae, flattened areas between 5th legs distinct and subconical; sternum of segment 6 convexly depressed between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna flattened and plate-like, with bicruciform impressions on segments 8-10 and variably wide, shallow, central depressions on remaining segments. Coxae with blunt tubercles on segments 9-15; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 3.3 mm wide and 1.8 mm long at midpoint, strongly indented anteriomediad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 106, of topotype) with acropodites angling anteriomediad and overlapping each other in midline of aperture, extending forward beyond anterior margin and inserting in depression between 7th legs. Gonopod structure as follows (Figs. 107-108): Prefemoral process long, wide, and bisinuately curved, about half as long as basal zone, tapering smoothly and continuously to subacuminate tip, latter directed toward distal zone. Acropodite moderately thick and heavy, blade like, becoming progressively thinner and narrower beginning at anterior bend, configuration an inverted L; basal zone long, gently curved anteriad; anterior bend sharp, well defined; peak flattened, angling slightly downward, distal half narrowing strongly; apical curve broad, poorly defined; distal zone short, curving directly laterad, coplanar with peak and obscured in medial view, narrowing slightly distad and expanding apically into blunt tip; latter bent slightly downward from distal zone, with produced inner corner resembling inverted reflexed condition. Medial flange arising on distal extremity of basal zone, extending across anterior bend and terminating on distal extremity of peak, broadest distad. Lateral flange arising on peak and terminating at same position as medial flange. Prostatic groove running along inner surface of basal zone, crossing to lateral side at anterior bend and continuing to opening on inner corner of tip.

Female Paratype. — Length 46.7 mm, maximum width 10.8 m, W/L ratio 23.2%, depth/width ratio 67.6%. Agreeing closely with males in somatic features, except ends of collum not produced beyond those of following tergite. Cyphopods *in situ* with openings of valves visible in aperture. Receptacle small, flat, located beneath medial corners of valves, surface finely granular. Valves large, equal, with broad central depression, surfaces finely granulate.

Variation. — No differences are apparent between the topotype and the described paratype. In the male from Burrville the prefemoral process is a little narrower and the basal zone straighter, but otherwise it agrees with that from Sunbright.

Ecology. — Keeton (1960) gave no indication of habitat in his description, but the topotypes I collected were found under deep piles of oak leaves in shallow ravines. There are no cove habitats or rhododendron at this site or at Burrville, and investigations in such environments near Wartburg, Oakdale, and Frozen Head State Park yielded an abundance of *Brachoria* but none of *picapa*. Thus, *picapa* is not a cove species and has different ecological preferences.

Distribution. — Known only from the type and paratype localities near Sunbright and Burrville in the Cumberland Plateau of northern Morgan County, Tennessee.

Remarks. — Although the paranota of males continue the slope of the dorsum and can be described as moderately depressed, they angle more sharply ventrad than in most congeners. Males of *picapa* thus appear thicker and more highly arched or vaulted than most *Sigmoria* males.

The medial view of the gonopod (Fig. 107) was prepared from more anterior and dorsal angles than usual to show the tip, which is coplanar with the peak and obscured by the latter in strictly medial perspective. The acropodite therefore appears to extend well beyond the level of the prefemoral process, but it really does not as shown in lateral view (Fig. 108). Although they are over 80 miles and two physiographic regions apart, the configuration of the prefemoral process of *picapa* more closely resembles that of *prolata* than those of any other Cumberland species.

I visited the type locality twice in 1979 and once in 1980 with my assistants to search for topotypical males. They were harder to find than any other species of *Sigmoria s. lat.*, and around 40 man hours were required for the two specimens, which were finally discovered on the third trip. Investigations north of the known area in Fentress and Scott counties and the adjacent part of Kentucky were unproductive, although there is an abundance of ostensibly desirable sites.

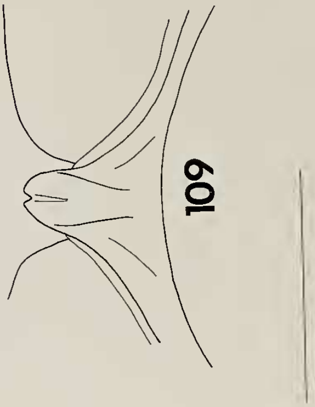
The *Mimetica* Group

With three species in the Nashville Basin and the eastern Highland Rim of central Tennessee, the *mimetica* group forms the western distributional limit of *Sigmoria s. lat.* The species have thick, sturdy acropodites, and next to *rileyi* and *abbotti, crassicurvosa* and *pendulata* have the most massive in the genus. The telopodite is oriented differently on the coxa, so that the inner surface of the basal zone is directed mediad instead of anteriomediad, and the peak is also tilted laterad exposing the undersurface in medial view. Because of these changes, the prostatic groove is visible in medial view from its origin on the prefemur to the apical curve or distal zone. The lateral flange is absent and the medial flange appears to be also, but I think it is represented by a slightly wider margin along the peak that is inconspicuous in medial view because of the tilting. It can be seen in a ventral examination of the peak but is poorly demarcated from the acropodite stem, and its origin and termination are indistinct. In the interests of consistency, I report it as located on the peak. Prefemoral processes are generally short to vestigial. Color hues are lighter than those of the Cumberland and Appalachian species. Red is replaced by pink, and the blue stripes are lighter with less of a grayish tint than occurs in other species.

Components. — *mimetica* (Chamberlin); *crassicurvosa,* new species; *pendulata,* new species.

Sigmoria (Falloria) mimetica Chamberlin Figs. 109-114

Fontaria mimetica Chamberlin, 1918a:29-30. Attems, 1938:167.
Sigmoria mimetica: Hoffman, 1950:6. Chamberlin and Hoffman, 1958:51.



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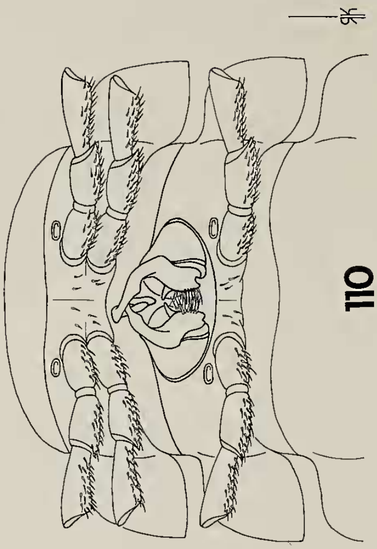

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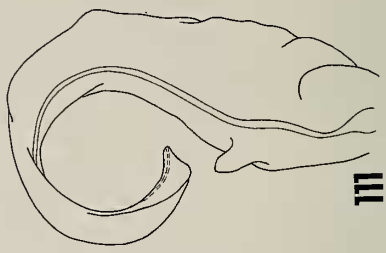

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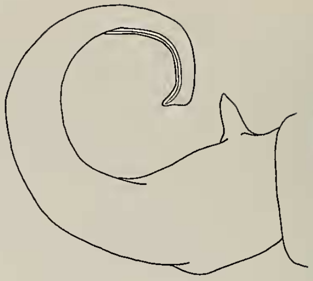

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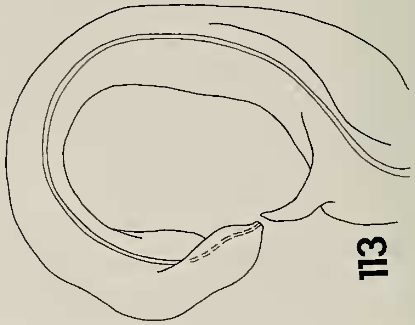

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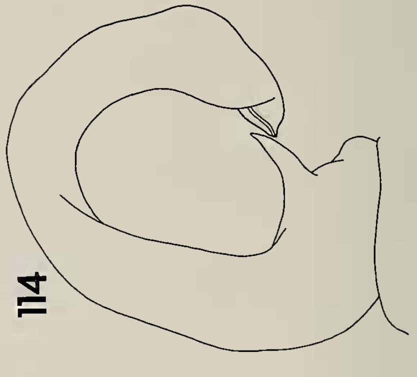


114

Type specimens. — Male holotype (RVC) collected by H. Cummins, 21 April 1917, from Glendale Hills south of Nashville, Davidson Co., TN. Hoffman (1950) and Chamberlin and Hoffman (1958) report that the type is in the MCZ collection, but it currently is located in the RVC. There is no section of Nashville by this name, but according to the Chamber of Commerce, it probably refers to the area near Glendale Lane and the communities of Oak Hill and Forest Hills in south Nashville. This area, just north of the Williamson County line, contains Lake Radnor State Park, and the specimens from there are considered topotypes.

Diagnosis. — A moderate-size species of *Sigmoria* with narrow medial flange located on peak and with pink paranota and usually blue metatergal stripes; gonopods with following diagnostic characters: acropodite moderately thick and heavy, arch high and rounded, extending beyond level of prefemoral process; basal zone with inner surface directed mediad, with small, rounded distomedial lobe; anterior bend and apical curve poorly defined; peak tilted laterad, exposing undersurface in medial view; distal zone long, curving broadly into arch and extending nearly to proximal part of basal zone, coplanar with latter, twisted near midlength; tip blunt, located on inner corner of distal zone; medial flange narrow and inconspicuous in medial view, located on peak, with small, rounded distal lobe; lateral flange absent.

Color in Life. — Paranota pink; metaterga black, with blue (occasionally white) transverse stripes along caudal margins connecting paranotal spots; collum with or without concolorous blue or white stripe on anterior edge.

Holotype. — Body fragmented, see topotype description for measurements.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.5 mm; interantennal isthmus 1.8 mm. Antennae reaching back to middle of third paranota; relative lengths of antennomeres $2>3>4=6=5>1>7$. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and frontal absent, clypeal about 10-10, labral about 12-12, merging with clypeal series and continuing for short distances along genal margins.

Terga smooth, polished, with only faint wrinkling. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded on collum but moderately acute thereafter. Peritremata low on anterior segments, becoming sharp and distinct in midbody region. Ozopores located in caudal half of peritremata, opening dorsad.

FIG. 109-114. *Sigmoria (Falloria) mimetica.* 109, process of 4th sternum of holotype, caudal view. 110, gonopods *in situ,* ventral view of topotype. 111, telopodite of left gonopod of holotype, medial view. 112, the same, lateral view. 113, telopodite of left gonopod of male from 11 mi. E. Lebanon, Wilson Co., TN, medial view. 114, the same, lateral view. Scale line for fig. 110 = 1.00 mm; line for other figs. = 1.00 mm for 113-114; 1.33 mm for 109; 1.78 mm for 111-112.

Process of 4th sternum shorter than widths of adjacent coxae and divided apically (Fig. 109); of segment 5, produced into pair of small, paramedial knobs between 4th pair of legs and lower, more rounded lobes between 5th legs; of segment 6, convexly recessed between both leg pairs to accommodate gonopodal acropodites. Postgonopodal sterna relatively flat, with shallow transverse grooves originating between leg pairs. Coxae without ventrodistal spines or tubercles on all legs; prefemoral spines beginning on segment 6, becoming longer and sharper caudally.

Gonopodal aperture rounded, 3.1 mm wide and 2.1 mm long at midpoint, without indentations on anteriolateral margins, sides flush with metazonal surface, caudal margin slightly thickened. Gonopods *in situ* (Fig. 110, of topotype), with acropodites curving anteriomediad over aperture, overlapping and bending abruptly dorsad apically, extending beyond anterior margin of aperture to between 7th legs. Gonopod structure as follows (Figs. 111-112): Prefemur with short prefemoral process directed toward distal zone of acropodite, sides parallel, tapering apically to central tip. Acropodite moderately thick and heavy, arch high and rounded, overhanging and extending well beyond level of prefemoral process; basal zone relatively long and broad, situated with inner surface directed mediad, with small, rounded distomedial lobe; anterior bend broad, poorly defined; peak relatively short, high and rounded, tilted laterad exposing undersurface in medial view; apical curve broad, poorly defined; distal zone long, coplanar with basal zone, curving broadly into arch, extending nearly to base of acropodite just above level of prefemoral process and directed toward basal zone, twisted slightly near midlength producing additional surface on medial side; tip subacuminate, located on inner corner of distal zone, suggesting reflexed condition. Medial flange narrow and inconspicuous, located on peak but possibly incorporating lobe on basal zone. Lateral flange absent. Prostatic groove running along inner surface of acropodite, entirely visible in medial view until reaching distal zone.

Male Topotype. — Length 36.2 mm, maximum width 9.6 mm, W/L ratio 26.5%, depth/width ratio 46.9%. Segmental widths as follows:

collum 7.1 mm	13th 9.2
2nd 8.0	14th 9.0
3rd 8.9	15th 8.5
4th 9.2	16th 7.0
5th-7th 9.4	17th 6.6
8th-12th 9.6	18th 4.9

The topotypes agree closely with the holotype in somatic and gonopodal features. The only noticeable difference is that the prefemoral process is slightly longer.

Female Topotype. — Length 36.0 mm, maximum width 9.3 mm, W/L 25.8%, depth/width 65.6%. Agreeing closely with holotype in somatic features, except ends of collum not produced beyond those of following segment. Cyphopods *in situ* with corners of receptacles visible in aperture, valves directed anteriolaterad. Receptacle large, situated along bases of valves, surface rugulose but smooth. Valves moderate and equal, surfaces finely granulate.

Variation. — The gonopods of *mimetica* are quite uniform. The length of the prefemoral process varies and the arch may be broader than in the holotype, but these minor differences occur randomly throughout the range. On the eastern edge of the range, 11 mi. E Lebanon, Wilson County, occurs the different form shown in figures 113-114. The prefemoral process tapers smoothly and continuously throughout the length, rather than just apically, and the acropodite has rounded lobes on the lateral margin at the apical curve and another one just proximal to the tip, which is blunt. The distal zone is directed toward the prefemoral process instead of the basal zone. I believe it is a relict of a former faunal connection between *mimetica* and *crassicurvosa,* and it may be extinct, as this area has been examined three additional times without success. Since it occurs on the range periphery of *mimetica,* I include it under this species.

Ecology. — I have taken *mimetica* under thin layers of leaves on relatively hard substrates near water sources. Some samples, for example those in Henry Horton and Cedars of Lebanon State Parks, were remote from water but still met the other ecological criteria.

Distribution. — An area about 60 miles long and 50 miles wide in the Nashville Basin and adjacent fringe of the Western Highland Rim of central Tennessee. All specimens have been taken north of the Duck River, and the range traverses the Cumberland River. I have not encountered *mimetica* in the Eastern Highland Rim Province or in Kentucky, although the Robertson and Macon County localities are only about 10 miles south of the state line. Specimens were examined as follows:

TENNESSEE. — *Robertson Co.,* 3 mi. E Springfield, along TN hwy. 76, 2.2 mi. E jct. TN hwy. 49, M, F, 12 June 1979 (NCSM A2753). *Summer Co.,* 1.7 mi. S. Bransford, 3M, 3F, 20 April 1958, L. Hubricht (RLH). *Macon Co.,* 4 mi. SW Lafayette, 2M, F, 26 April 1958, L. Hubricht (RLH). *Cheatham Co.,* 3.6 mi. N Ashland City, along TN hwy. 49, 3.6 mi. N jct. TN hwy. 12, 4M, 6F, 12 June 1979 (NCSM A2758). *Davidson Co.,* 6 mi. SE Ashland City, along TN hwy. 12 at Cheatham Co. line, 2F, 12 June 1979 (NCSM A2759); Glendale Hills S Nashville, M, 21 April 1917, H. Cummins (RVC) TYPE LOCALITY; and Lake Radnor St. Pk., 6M, 2F, 12 June 1979 (NCSM A2761). *Wilson Co.,* 11 mi E Lebanon, 2M, 25 June 1957, L. Hubricht (RLH); 12.8 mi. NNE Lebanon, along US hwy. 70N, 0.8 mi. W Smith Co. line, M, 2F, 28 May 1980 (NCSM A3167); and Cedars of Lebanon St. Pk., 10M, 3F, July 1958, R.M. Sinclair (RLH) and 3M, 16 June 1976 (NCSM A876). *Cannon Co.,* 5.0 mi. NW Woodbury, along TN hwy. 145, 4.8 mi. N jct. US hwy. 70S, 4M, 3F, 9 May 1979 (NCSM A2653). *Williamson Co.,* "beyond Glendale," M, 14 October 1916, H. Cummins (RVC). *Maury Co.,* 6.3 mi. ENE Columbia, along TN hwy. 99, 5.5 mi. E jct. US hwy. 31, M, 10 May 1979 (NCSM A2662). *Marshall Co.,* Henry Horton St. Pk., campground area, 12M, 8F, 9 May 1979 (NCSM A2660).

Remarks. — In addition to the holotype, Chamberlin (1918a) also reported a female of *mimetica* from Hillsboro Hills, Nashville, and a male from "beyond Glendale." Both are present in the Chamberlin collection, but the female could be of *Brachoria glendalea* (Chamberlin), which is sympatric with *mimetica* in southern Davidson County. Since the area thought to represent Glendale Hills touches the Williamson County line, the male from "beyond Glendale" is considered to be from this county and is so cited above.

Sigmoria (F.) mimetica is the westernmost species in the genus, and the collection from Cheatham County, specifically, constitutes the range limit.

I have sampled intensively over 40 miles farther west to the Tennessee River, and sporadically another 85 or so miles to the Mississippi River, to confirm that no congeners exist in this direction.

Sigmoria (Falloria) crassicurvosa Shelley, new species Figs. 115-120

Type specimens. — Male holotype (NCSM A2750) and 2 male and 3 female paratypes collected by R.M. Shelley and R.K. Tardell, 11 June 1979, from Smith Co., TN, 2.0 mi. W Carthage, along TN highway 25, 1.2 mi. W junction with TN highway 85. Male and female paratypes deposited in FSCA.

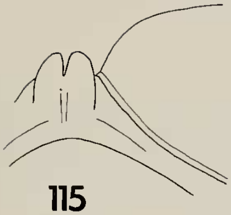
Diagnosis. — A moderate-size species of *Sigmoria* with narrow medial flange located on peak and with pink paranota and blue transverse metatergal stripes; gonopods with following diagnostic characters: prefemoral process variable, short and acute or vestigial; acropodite thick and massive, broadly curved and subtending rectangular arch, extending well beyond level of prefemoral process; basal zone with inner surface directed mediad, with or without ledge on medial surface; anterior bend and apical curve sharp, well defined; peak gently curved, tilted laterad, exposing undersurface in medial view, with or without distal expansion on lateral surface; distal zone equal in length to and coplanar with basal zone, either parallel to latter and bent into arch near midlength or angling into arch, configuration variable, with or without proximal indentation on lateral surface, broadly rounded lobe at midlength on medial side, and terminal medial lamina; tip elongated and acuminate, with converging striae.

Color in life. — Paranota pink; metaterga black with blue transverse stripes along caudal margins connecting paranotal spots; collum with concolorous blue stripes along anterior and posterior edges.

Holotype. — Length 36.2 mm, maximum width 9.0 mm, W/L 24.9%, depth/width ratio 53.2%. Segmental widths as follows:

collum	6.4 mm	15th	8.7
2nd	7.8	16th	7.9
3rd	8.5	17th	6.8
4th	8.9	18th	5.3
5th-14th	9.0		

FIGS. 115-120. *Sigmoria (Falloria) crassicurvosa.* 115, process of 4th sternum of holotype, caudal view. 116, gonopods *in situ,* ventral view of paratype. 117, telopodite of left gonopod of holotype, medial view. 118, the same, lateral view. 119, the same, subdorsal view. 120, telopodite of left gonopod of male from Dekalb Co., TN, medial view. Scale line for fig. 116 = 1.00 mm; line for other figs. = 0.80 mm for 119; 1.00 mm for 117-118 and 120; 1.33 mm for 115.



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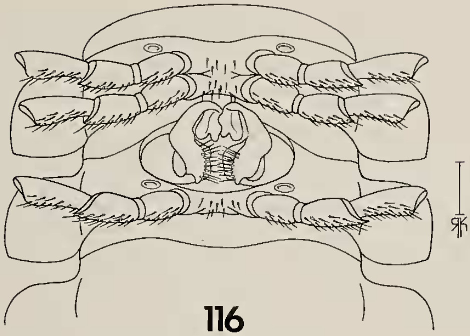

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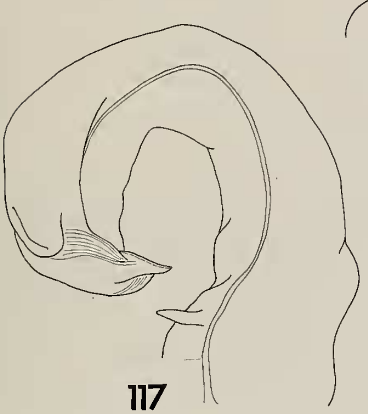

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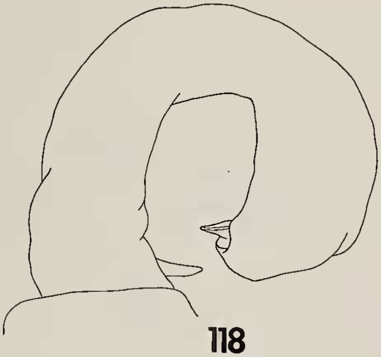

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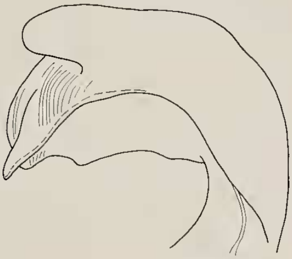

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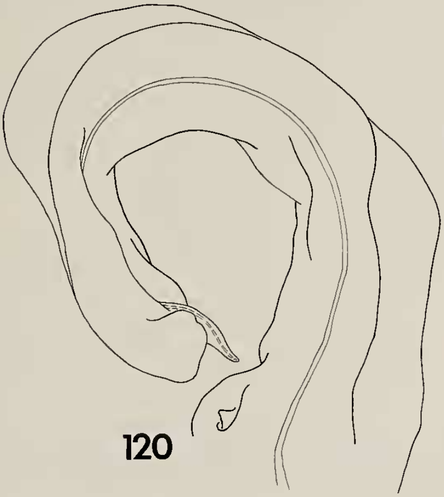

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Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.4 mm, interantennal isthmus 1.3mm. Antennae reaching back to middle of 3rd paranota, relative lengths of antennomeres 2> 3> 4 = 5> 6> 1> 7. Genae with distinct impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 10-10, labral 12-12.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, ends not produced beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 5, blunt on 6-12, becoming progressively more acute posteriorly. Peritremata flat on anterior segments, becoming elevated and distinct on segment 6. Ozopores located near middle of peritremata, opening dorsad.

Sternum of segment 4 with small, divided process, much shorter than widths of adjacent coxae (Fig. 115); that of segment 5 with two conical paramedian knobs between 4th legs, much shorter than adjacent coxal widths, and two low elevated areas between 5th legs; that of segment 6 strongly and convexly depressed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna flattened and platelike, with bicruciform impressions on segments 8-9 and shallow central impression thereafter. Coxae with low, rounded tubercles on segments 10-12; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.0 mm wide and 1.3 mm long at midpoint, without indentations, sides flush with metazonal surface. Gonopods *in situ* (Fig. 116, of paratype) with acropodites curving anteriad entirely over aperture, angling slightly toward midline and touching or slightly overlapping in apical curve regions. Gonopod structure as follows (Figs. 117-119): Prefemoral process short and acute, directed towards coxa. Acropodite thick and massive, heavily sclerotized, broadly curved but subtending rectangular arch, overhanging and extending well beyond level of prefemoral process; basal zone with inner surface directed mediad, relatively long and straight, without modifications; anterior bend sharp, well defined; peak relatively long, gently curved, tilted laterad exposing undersurface in medial view; apical curve sharp, well defined; distal zone long, equal in length and coplanar with basal zone, with broadly rounded lobe distad on medial side, bent inward into arch apically; tip broadly rounded on lateral side, with striae on both lateral and medial sides converging onto elongated, acuminate medial corner. Medial flange narrow and indistinct, located on peak. Lateral flange absent. Prostatic groove running along medial and inner surfaces of acropodite to terminal opening.

Male paratypes. — The male paratypes agree with the holotype in all particulars.

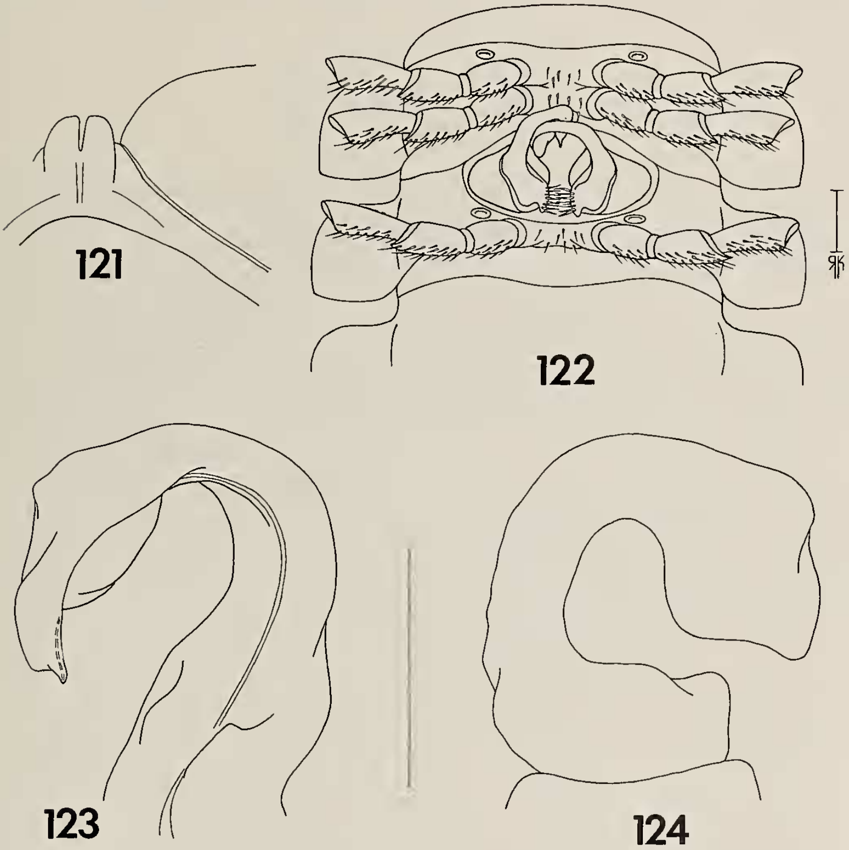
Female paratype. — Length 42.5 mm, maximum width 10.1 mm, W/L 23.8%, depth/width ratio 64.4%. Cyphopods *in situ* with corners of valves and receptacles visible in apertures, valves directed anteriolaterad. Receptacle large, situated along bases of valves, surface rugulose but smooth. Valves moderate and equal, surfaces finely granulate.

Variation. — The Dekalb County males differ considerably from the types as shown in figure 120. The prefemoral process is a vestigial nub and barely detectable on the massive prefemur. There is a ledge along the medial surface of the basal zone that is broadest distad and might represent part of the medial flange. The peak is expanded distad into a rounded lateral margin, which is indented on the proximal part of the distal zone. This section of the acropodite is straight and angles toward the basal zone instead of being parallel as in the holotype. Apically, there is no medial lobe on the distal zone, but there is a terminal lamina which obscures the proximal part of the solenomerite in medial view.

Ecology. — *Sigmoria (F.) crassicurvosa* occurs under thin layers of ves on relatively hard substrates near water sources.

Distribution. — Known only from the following three localities on the stern edge of the Nashville Basin.

ENNESSEE. — *Smith Co.,* 2 mi. W Carthage, along TN hwy. 25, 1.2 mi. W jct. TN hwy. 3M, 3F, 11 June 1979 (NCSM A2750) TYPE LOCALITY; and 7 mi. SW Carthage, along umbered rd. off TN hwy. 141, M, F, 28 May 1980 (NCSM A3170). *Dekalb Co.,* 5 mi. W Smithville, along US hwy. 70, 3M, 9 May 1979 (NCSM A2648).



FIGS. 121-124. *Sigmoria (Falloria) pendulata.* 121, process of 4th sternum of holotype, caudal view. 122, gonopods *in situ,* ventral view of paratype. 123, telopodite of left gonopod of holotype, medial view. 124, the same, lateral view. Scale line for fig. 122 = 1.00 mm; line for other figs = 1.00 mm for 123-124; 1.33 mm for 121.

Sigmoria (Falloria) pendulata Shelley, new species Figs. 121-124

Type specimens. — Male holotype (NCSM A2650) and 5 male and 5 female paratypes collected by R.M. Shelley and R.K. Tardell, 9 May 1979, from Edgar Evins State Park, Dekalb Co., TN. Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on peak and with pink paranota and usually blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process absent or varying in size to moderately long and acute; acropodite thick and massive, arch an

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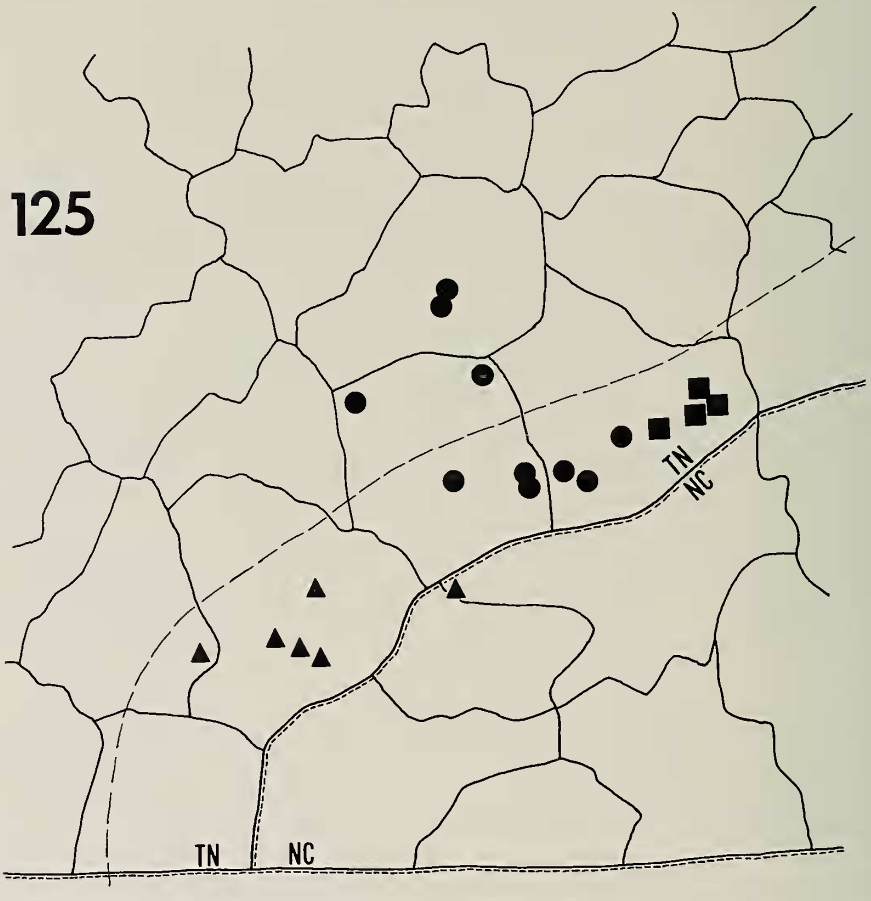


FIG. 125. Distributions of *ainsliei*, dots; *aphelorioides*, triangles; and *prolata*, squares, in western North Carolina and eastern Tennessee. The dashed line is the approximate boundary between the Blue Ridge and Ridge and Valley Provinces.

inverted U, extending well beyond level of prefemoral process; basal zone with inner surface directed mediad; anterior bend and apical curve well defined; peak high and rounded, tilted laterad; distal zone coplanar with and equal in length to basal zone, with expansion at midlength on anterior side extending onto medial and lateral surfaces and forming lobes, curved slightly inward distad and tapering to blunt tip.

Color in Life. — Paranota pink; metaterga black with blue, occasionally yellow, stripes along caudal margins connecting paranotal spots; collum with pink stripe along anterior edge and blue along posterior.

Holotype. — Length 33.9 mm, maximum width 9.0 mm, W/L ratio 26.5%, depth/width ratio 69.7%. Segmental widths as follows:

collum	6.4 mm	8th-14th	9.0
2nd	7.6	15th	8.5
3rd	8.3	16th	8.0
4th	8.5	17th	6.5
5th-7th	8.8	18th	4.6

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.7 mm, interantennal isthmus 1.4 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>6>4>1>7. Genae with shallow central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal 12-12.

Terga smooth, polished, with only faint wrinkling on anterior parts of paranota. Collum broad, ends extending slightly beyond those of adjacent tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 5, blunt on 6-12, becoming progressively more acute posteriorly. Peritremata sharp and distinct on all segments, clearly elevated above metazonal surface, ozopores located near middle of peritremata, opening dorsolaterad.

Sternum of segment 4 with minute, divided projection, much shorter than adjacent coxal widths (Fig. 121); that of segment 5 with two low rounded knobs between 4th legs, much shorter than adjacent coxal widths, and broad flattened elevations between 5th legs; that of segment 6 deeply and convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna flattened and plate-like, bicruciately impressed on segments 8-9 and with variably broad, shallow central impressions on remaining segments. Coxae with low rounded tubercles beginning on segment 8; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 3.5 mm wide and 1.8 mm long at midpoint, without indentations, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 122, of paratype) with acropodites extending anteriomediad and peak of one overlapping apical curve of other, apical curve of former extending slightly beyond anterior margin of aperture and inserting in depression between 7th legs. Gonopod structure as follows (Figs. 123-124): Prefemoral process absent, with only a lowly rounded ridge at this position on prefemur. Acropodite thick and massive, heavily sclerotized, subtending symmetrical, inverted U shaped arch, overhanging and extending well beyond prefemur; basal zone moderately long, inner surface directed mediad; anterior bend sharp, well defined, continuous through peak with distal zone; peak short, high, and rounded, apex at midlength, continuing curvature of arch, tilted only slightly laterad; apical curve sharp, well defined; distal zone long, coplanar with and nearly equal in length to basal zone, with broadly rounded swelling at midlength on anterior side extending onto medial and lateral surfaces thus producing lobe-like effect at this point, slightly curved beyond swelling and tapering to blunt termination, directed toward cannula of coxa; tip located on produced inner corner of distal zone. Medial flange narrow, located on peak, indistinct in medial view. Lateral flange absent. Prostatic groove running along inner surface of basal zone and under surface of peak to opening at tip of distal zone.

Male Paratypes. — The male paratypes agree with the holotype in all structural details. In color, however, four specimens had yellow metatergal stripes as opposed to the blue stripes of the holotype and one paratype.

Female Paratype. — Length 37.9 mm, maximum width 10.3 mm, W/L ratio 27.2%, depth/width ratio 67.9%. Cyphopods *in situ* with corners of valves and receptacles visible in apertures, valves directed anteriolaterad. Receptacle large, situated along bases of valves, surface rugulose but smooth. Valves moderate and equal, surfaces finely granulate.

Variation. — Color varies only in the type series. All other specimens have blue metatergal stripes connecting pink paranotal markings.

Males in the eastern edge of the range in Putnam County possess long, acute prefemoral processes that extend nearly to the levels of the distal

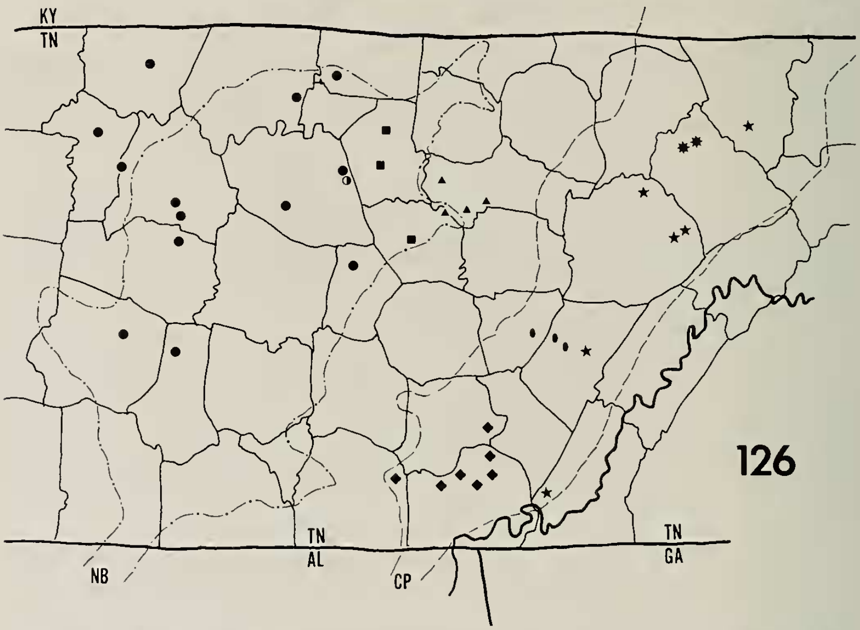


FIG. 126. Distribution of the subgenus *Falloria* in central Tennessee. Dots, *mimetica;* half shaded dot, atypical population, possible remnant of intergrades between *mimetica* and *crassicurvosa;* squares, *crassicurvosa;* triangles, *pendulata;* asterisks, *picapa;* stars, *forficata,* ovals, *abbreviata;* diamonds, *houstoni.* The dashed lines show the approximate boundaries of the Cumberland Plateau Province (CP), and the Nashville Basin (NB) is denoted by a line of alternating dots and dashes. The intervening area, which curves northward over the Nashville Basin and continues on the western side, is the Highland Rim. The heavy line in the southeastern (lower right) corner represents the course of the Tennessee River.

zones, and there is a geographic trend toward a longer and larger structure from west to east. The types and the most proximal sample from western Putnam County lack the process, and it is short but distinct in sample A3176, from an intermediate locality. However, no changes are evident in the acropodites.

Ecology. — *Sigmoria (F.) pendulata* occurs under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — Known only from an area about 13 miles long and 8 miles wide in the eastern Highland Rim. Specimens were examined as follows:

TENNESSEE. — *Dekalb Co.,* Edgar Evins St. Pk., 6M, 5F, 9 May 1979 (NCSM A2650-2651) TYPE LOCALITY. *Putnam Co.,* 12 mi. W Cookeville, along US 70N at Lafayette Twp., 2M, 7F, 10 June 1979 (NCSM A2748); 14.3 mi. SW Cookeville, along co. rd. 6162, 0.3 mi. S TN hwy. 141, 5M, 4F, 28 May 1980 (NCSM A3176); and 9.5 mi. SSW Cookeville, Burgess Falls area on Falling Water Rd., 3M, 2F, 29 May 1980 (NCSM A3178).

Remarks. — Approximately 17 miles separate the ranges of *pendulata* and *mimetica,* and if the swelling on the distal zone of *pendulata* were removed, its acropodite would be very close to that of the latter except for slightly less curvature in the distal zone.

Part II: Revision of Deltotaria

by Rowland M. Shelley

Taxonomic Characters

Hoffman (1961) cited two diagnostic features for *Deltotaria,* the coxal apophysis and the absence of frontal and vertigial (epicranial) facial setae. However, many apheloriine xystodesmids lack epicranial setae, and with much more material at my disposal, I can report that frontal setae are present on most individuals of both sexes of *Deltotaria.* Thus, the only truly diagnostic generic character is the subconical coxal apophysis. Hoffman also reported that the gonocoxae were connected by a partially sclerotized sternal remnant, which would be a second such feature as this was one of the traits cited for the tribe Rhysodesmini (Hoffman 1960). However, I have carefully examined a number of males of both species and found that although the membrane joining the coxae is occasionally quite tough and difficult to tear, there is no evidence of sclerotization. *Deltotaria* thus conforms to contribal genera in lacking a sternal remnant. Hoffman also regarded the form of the caudolateral corner of the paranota as significant at the specific level, since the peritremata are prolonged slightly beyond the caudal edge in some forms to produce a small projection. However, this occurs widely in the Apheloriini and is insignificant. As with most apheloriine genera, the taxonomically important characters in *Deltotaria* involve chiefly the male gonopods. The two species are differently colored, as indicated below, but the pregonopodal sternal processes are nearly identical and insufficiently different from conditions in sympatric species to be useful in generic determinations.

Coloration. — Both species exhibit the metatergal stripe pattern characteristic of many forms of *Sigmoria s. lat.*, but *lea* Hoffman, in the Piedmont Plateau, is exclusively yellow, whereas *brimleii* Causey, in the southern Blue Ridge Province, displays various shades of red and orange. There is also an unusual aspect to the colors of *lea* and southern specimens of *brimleii philia* (Chamberlin) that was first reported by Filka and Shelley (1980). Whereas many xystodesmids display a glossy, highly polished finish, there is a sparkle or glitter to the pigments of these forms of *Deltotaria* that is much like that of metallic paint. This sheen of *lea* allows for positive identifications of even females in the field and thus is diagnostic for both the species and the genus in the Piedmont Plateau. The difference is unmistakable and readily apparent if one compares live specimens of *D. lea* and sympatric, yellow striped intergrades of *Sigmoria (Sigmoria) latior.*

Gonopodal Characters. — In the terminology I have developed for "sigmoid" gonopods, what Hoffman (1961) labeled a subterminal lobe or process and identified by the letter "B" is really the lateral flange, and what he considered the solenomerite is actually the part of the distal zone distal to the flange. To date, all gonopodal drawings of *Deltotaria* have also been from a somewhat ventrolateral aspect since this view best reveals the coxal apophyses. Consequently, the medial flanges have yet to be illustrated or described. These lamellae clearly reveal the generic affinity between *Deltotaria* and *Sigmoria s. lat.*, and the locations are diagnostic at the specific level. I therefore present medial views of all illustrated gonopods to highlight this as yet unrevealed feature.

The coxal apophysis is the only truly diagnostic generic character, as the gonopods would otherwise be readily referrable to *Sigmoria s. lat.* This projection arises anteriolaterad on the coxa and extends directly ventrad. The length and configuration are useful at the specific level, and as viewed in medial and lateral profiles, there are two basic types — broadly triangular with sides narrowing rapidly to a subacuminate tip, and long and slender with sides roughly parallel through most of the length except apically. Triangular apophyses obtain in *lea,* where the projection is short and terminates below the level of the prefemur, and the nominate subspecies of *brimleii,* where it is moderately long and extends to the level of the prefemoral process. In *b. philia* the process is slender and much longer, stretching to or beyond the level of the tip of the acropodite and thus well beyond the prefemoral region. Despite the clear distinctions in the coxal apophyses, I do not believe the two forms of *brimleii* are reproductively isolated, as there is evidence of intergradation and there are no significant acropodal differences.

On the acropodites, specific differences obtain in the apical thickness, the curvature of the distal zone, and the locations and shapes of the medial and lateral flanges. *Deltotaria lea* has a decidedly stronger, thicker, and heavier acropodite than does *brimleii,* particularly in the distal zone, which is broad and spatulate in the former and thin and fragile in the latter. Accordingly, *lea* is apically blunt whereas *brimleii* is subacuminate. In curvature, the distal zone extends downward from the peak in *lea* and is coplanar with the basal zone. In *brimleii,* however, the section projects laterad to varying degrees, is not coplanar with the basal zone, and in a few individuals is nearly coplanar with the peak. All forms of *Deltotaria* have a medial flange, but in *lea* it is broadly expanded and located on the basal zone, whereas in *brimleii* it is narrow and located on the peak and/or distal zone. In *lea* the flange is curved to form a concave inner surface on the basal zone. In *brimleii* the flange is level or straight with sometimes a gently rounded margin, but it is comparatively indistinct and poorly demarcated from the acropodite stem. The lateral flange is absent from *lea* and present in *brimleii,* where there is a general trend toward smaller flanges in a southerly direction. In northern populations the lateral flange is produced into lobes of varying lengths and shapes, but in *b. philia* at the southern periphery, it is narrow, indistinct, and poorly demarcated from the acropodite stem. Here, the flange imparts a hastate appearance to the acropodite and is best detected in profile by examining the distal zone from a ventral perspective.

Genus DELTOTARIA Causey

Deltotaria Causey, 1942:165. Chamberlin and Hoffman, 1958:29. Hoffman, 1961:22-25; 1979:158. Jeekel, 1971:258.

Phanoria Chamberlin, 1949:101. Jeekel, 1971:279

Type species. — Of *Deltotaria, D. brimleii* Causey, 1942, by original designation; of *Phanoria, P. philia* Chamberlin, 1949, by original designation.

Diagnosis. — Characterized by the variably triangular or elongate coxal apophysis.

Color in Life. — Paranota red, orange, or yellow; metaterga black with concolorous red, orange, or yellow stripes along caudal margins connecting paranotal spots; collum with stripes along anterior or both margins; colors sometimes with sparkling, metallic sheen.

Description. — Head of normal appearance, smooth, polished. Epicranial suture shallow, distinct, terminating in interantennal region; interantennal isthmus moderately wide; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article, no other sensory structures apparent. Facial setae reduced; epicranial and interantennal absent; frontal and genal present or absent, clypeal and labral present.

Terga generally smooth, polished, becoming moderately coriaceous on anterior halves of paranota. Collum variably broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, generally continuing slope of dorsum, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody region and progressively more acute posteriorly. Peritremata generally indistinct, slightly elevated above paranotal surfaces; ozopores located caudal to midlength, opening dorsolaterad. Prozonites smaller than metazonites; strictures distinct, smooth.

Caudal segments normal for family.

Sides of metazonites smooth or irregular, with varying shallow, curved impressions. Strictures sharp, distinct. Pregonopodal sterna of males modified as follows: that of segment 4 with small to moderate, apically divided process between 3rd legs, shorter than widths of adjacent coxae; that of segment 5 with small projections between anterior legs and variable elevated areas between posterior ones; that of segment 6 with variable convex recession between caudal legs to accommodate apices of acropodites when body segments compressed, 7th legs sometimes set slightly farther apart than 6th. Postgonopodal sterna generally flat and unmodified, with shallow grooves on those immediately posterior to 7th segment and shallow central impressions on rest. Gonapophyses on 2nd leg pair of males distinctly elevated above coxal surfaces, with round, apical knobs. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Coxae with low tubercles beginning on postgonopodal legs, becoming progressively longer and sharper caudally; prefemoral spines beginning on segment 5, becoming longer and more acute caudally; tarsal claws bisinuate. Hypoproct variable, subtriangular to rounded; paraprocts with margins strongly thickened.

Gonopodal aperture ovoid to elliptical, with slight indentation anteriolaterad, front flush with metazonal surface, sides and caudal edge elevated. Gonopods *in situ* with acropodites projecting ventrad from aperture, curving anteriomediad and overlapping at various positions in midline, extending anteriad slightly beyond anterior margin of aperture. Coxae moderate, connected by membrane only, no sternal remnant, with subconical apophyses of variable lengths arising on anterior sides and projecting ventrad. Telopodite set terminally on coxa, latter not projecting distad beyond prefemoral region. Prefemora moderate, with or without variable prefemoral processes, latter occasionally vestigial. Acropodite moderately thick and heavy basally, becoming thinner and more fragile or spatulate distally, with torsion, curving through one or more vertical planes in vaguely sigmoidal configuration as seen *in situ* and in medial and lateral views, configurations as described for *Sigmoria s. lat.* Basal zone usually relatively long, around 1/3 of total acropodite length, inner surface directed anteriad, medial surface with or without broad, curved, laminate flange, latter forming convex inner surface. Anterior bend usually broad, poorly defined. Peak variable but usually relatively short and gently curved, apex near midlength, with or without variably narrow laminate flange on medial edge. Apical curve variable but usually broad, poorly defined. Distal zone of variable length and configuration, either broad and spatulate or with sides tapering smoothly and continuously, projecting downward from peak and coplanar with basal zone or not coplanar and extending laterad to various degrees, occasionally sharply curved into arch and lying beneath and parallel to peak; with or without variably narrow medial flange and variable lateral flange, latter ranging from long and rectangular to narrowly triangular to small and gently rounded; distal zone occasionally tilted mediad or laterad exposing medial or lateral flange in opposite perspective. Termination simple, blunt to acuminate. Prostatic groove arising in pit on prefemur, running along stem of acropodite and crossing from medial to lateral sides at various locations, opening terminally on tip of distal zone.

Females agreeing closely with males in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body. Cyphopodal aperture broad, encircling 2nd legs, sides slightly elevated above metazonal surfaces. Cyphopods *in situ* located lateral to 2nd legs, with corners of valves and receptacles visible in aperture. Receptacle small to moderate, located on medial sides of valves, surface rugulose to finely granulate. Valves small to moderate, subequal in size, directed caudolaterad, surfaces rugulose to finely granulate. Operculum minute, hidden under free end of valves.

Distribution. — Piedmont Plateau of west-central North and South Carolina between the Catawba and Broad rivers; and the southern Blue Ridge Province of North Carolina, Tennessee, Georgia, and South Carolina (Fig. 146). The range in the mountains extends onto the eastern and southern escarpments, but forms have not been encountered in the Piedmont proper. There is no tangible northern boundary in the mountains.

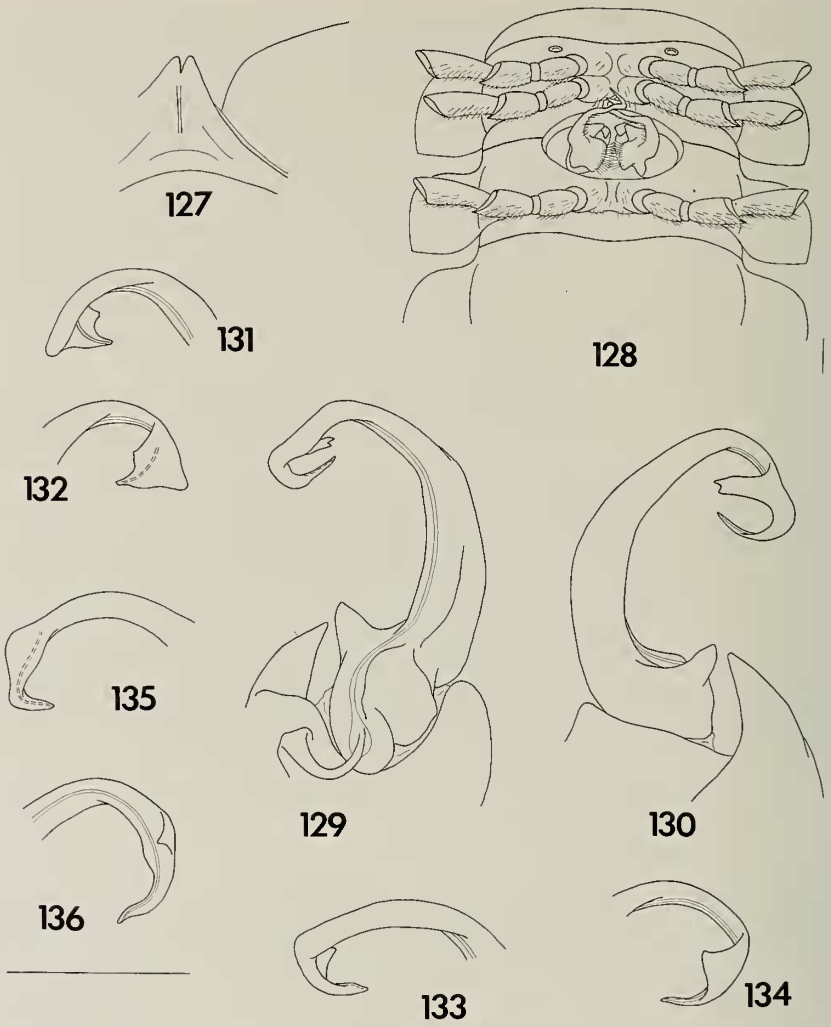
Species. — Two, one in each of the above described regions. Other workers may interpret the montane forms differently and recognize more reproductive isolates, but I doubt if any different species await discovery. *Deltotaria* thus resembles *Dynoria* in having two allopatric species, one in the Blue Ridge Province and one in the Atlantic lowlands (see Shelley 1984b).

Deltotaria brimleii Causey

Diagnosis. — Color of paranota and metatergal stripes varying from red to light orange, occasionally with sparkling, metallic sheen; coxal apophysis in profile broadly triangular to slender with sides nearly parallel, moderate to long, terminating at or beyond level of prefemoral process; acropodite distally slender and fragile; medial flange located on peak or proximal part of distal zone, with only slight lobe; lateral flange present, variable.

Ecology. — *Deltotaria brimleii* is a cove dwelling species.

Remarks. — *Deltotaria brimleii* occurs widely in the Southern Blue Ridge Province (Fig. 146). Five names have been proposed for forms in this area, but I think none are reproductively isolated. The only possible exception is the southernmost, occurring mainly in Georgia, for which the name *philia* was proposed by Chamberlin (1949). Its acropodite is basically the same as those of northern forms, and the narrow, indistinct lateral flange



FIGS. 127-136. *Deltotaria brimleii brimleii.* 127, process of 4th sternum of holotype, caudal view. 128, gonopods *in situ,* ventral view of male from Montreat, Buncombe Co., NC. 129, left gonopod of the same, medial view. 130, the same, lateral view. 131, distal half of acropodite of male from Bent Creek Forest Experiment Station, Buncombe Co., medial view. 132, the same, lateral view. 133, distal half of acropodite of male from Gatlinburg, Sevier Co., TN, medial view. 134, the same, lateral view. 135, distal half of acropodite of male from 8 mi. NW Brevard, Transylvania Co., NC, medial view. 136, the same lateral view. Scale line for fig. 128 = 1.00 mm; line for other figs. = 1.00 mm for each.

continues the general north to south clinal trend toward smaller laminae. However, *philia* is distinguished by the form of the coxal apophysis, which in profile is narrow with nearly parallel sides and extends to or beyond the level of the distal zone, well beyond the level of the prefemur. With one exception, all the other material has broadly triangular apophyses that terminate at the level of the prefemoral process. In this exception, from Chimney's Picnic Area, GSNMP, Tennessee, the process is intermediate in both length and shape. Because of this sample and the absence of meaningful acropodal differences, I think *philia* is only a geographic race and therefore recognize two subspecies based on the length and configuration of the coxal process. Three names are placed in synonymy under the nominate subspecies.

Deltotaria brimleii brimleii Causey, new status Figs. 127-136

Deltotaria brimleii Causey, 1942:165, Figs. 1-2. Chamberlin and Hoffman, 1958:30. Hoffman, 1961:25-28, Fig. 2c.

Deltotaria brimleardia Causey, 1950a:7-8, Figs. 2-3. Chamberlin and Hoffman, 1958:29.

Hoffman, 1961:30-31, Fig. 2b. **NEW SYNONYMY.**

Deltotaria tela Causey, 1950b:38-39, Figs. 3-5. Chamberlin and Hoffman, 1958:30. Hoffman, 1961:31-33, Figs. 1b, d, 2a. **NEW SYNONYMY.**

Deltotaria mariana Hoffman, 1961:28-30, Figs. 1a, e-h; 2d. **NEW SYNONYMY.**

Type specimen. — Male holotype (ANSP) collected by C.S. Brimley, 26 May 1923, at Swannanoa, Buncombe Co., NC. According to Hoffman (1961) there is a female topoparatype in the Causey collection, now at the FSCA. Hoffman presented a detailed description of the somatic aspects of the holotype, but as the genitalia are missing, he could only quote Causey's description (1942) and add a short interpretive comment. The following account of the pregonopodal sterna and the gonopods in "sigmoid" terminology is therefore prepared from a nearly topotypical male.

Diagnosis. — Coxal apophysis in profile moderately long and broadly triangular, extending to level of tip of prefemoral process, sides tapering rapidly to subacuminate tip; prefemoral process variable but usually present, occasionally vestigial.

Color in Life. — Paranota red; metaterga black with concolorous red stripes along caudal margins connecting paranotal markings; collum with red stripes along both anterior and posterior edges.

Male from Montreat, NC. — Fourth sterna with moderately long process between third legs, slightly shorter than widths of adjacent coxae (Fig. 127); segment 5 with minute paramedial knobs between 4th legs, much shorter than widths of adjacent coxae, and low rounded elevated areas between 5th legs; 6th sternum with slight recession along caudal edge to accommodate apical curvatures of acropodites.

Gonopodal aperture elliptical, 3.4 mm wide and 1.7 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 128) with acropodites extending anteriolaterad from aperture and peaks overlapping in midline, curving slightly over opposite side and anterior margin with tips crossing. Gonopod structure as follows (Figs. 129-130): Coxal apophysis curving caudad at midlength, directed toward prefemoral process and terminating just below tip of latter, apically subacuminate. Prefemoral process short, wedge shaped. Acropodite moderately thick and heavy basally, becoming thinner and more fragile distad, arch high and gently curved, overhanging and extending just beyond level of prefemoral process; basal zone long, bowed caudad; anterior bend broad, poorly defined; peak high and gently rounded, apex at midlength; apical curve sharp, well defined; distal zone moderately long, projecting strongly laterad from peak, not coplanar with basal zone, curving sharply caudad at midlength and lying under and parallel to peak in medial view, sides tapering smoothly and continuously to acuminate tip, latter directed toward anterior bend. Medial flange clearly demarcated from peak, moderately long, arising at midlength (apex), curving gently outward to form narrow lobe, terminating at distal extremity of peak, margins smooth. Lateral flange with broad, rectangular, proximal lobe, equal in length to distal half of distal zone, with two sharp apical teeth, sides smooth, lobe terminating at midlength, flange then curving gently to terminus near tip of distal zone. Prostatic groove crossing to lateral side at apex of peak, continuing to terminal opening.

Female from Polk Co., NC. — Length 34.1 mm, maximum width 7.8 mm, W/L ratio 22.9%, depth/width ratio 62.8%. Cyphopods with receptacle moderate, surface rugulose. Valves moderate, equal, surfaces rugulose.

Variation. — This subspecies includes all forms with a moderate coxal process. The lateral flange is highly variable and may be relatively laminate with a curvilinear margin or be produced into variable lobes, which may be rectangular, broadly or sharply triangular, or spiniform. The longest or rectangular lobes obtain in the northern part of the range, in the form named *brimleii* by Causey (1942). In the southern form named *mariana* by Hoffman (1961), the distal zone is tilted mediad exposing part of the lateral flange in medial view (Fig. 135). As noted by Causey (1950b) in the description and later by Hoffman (1961), the form named *tela* vaguely resembles *Sigmoria (Sigiria) rubromarginata* because the margin of the lateral flange is slightly produced, and the distal zone projects more strongly laterad, exposing part of the medial flange in lateral view (Fig. 132). It occurs chiefly in the Pisgah National Forest in Buncombe County, North Carolina, and occasional males from other areas approximate this configuration, for example in Cocke County, Tennessee. I do not find the resemblance with *S. rubromarginata* very striking and consider it convergence; however, it might reflect an ancestral connection. Overall in *b. brimleii* there is a north to south clinal progression toward smaller, less distinct lateral flanges, which culminates in the inconspicuous lamella of the other subspecies. Differences also obtain in the arch of the acropodite and the curve of the distal zone, which is directed more strongly laterad in the western part of the range.

Distribution. — The southern Blue Ridge Province from the Linville River to the Little Tennessee Rivers in North Carolina and the northeastern corner of Georgia, and, east-west, from the escarpment in North Carolina to the Great Smoky Mountains of Tennessee (Fig. 146). Most of the material comes from south of the Black Mountains in North Carolina. The two northernmost records represent gonopodal fragments found with paratypes of *Sigmoria aberrans* and *S. conclusa,* both synonymns of *l. latior (Sigmoria),* in the Chamberlin collection. They possess the lateral flange and general acropodal configurations that occur in the northern part of the range (similar to the form in Figs. 129-130) and the localities therefore seem plausible. However, confirmation with fresh material is desirable. Specimens were examined as follows:

NORTH CAROLINA. — *Burke Co.,* Linnville Falls, M (segments 7-8), 12 August 1910, R.V. Chamberlin (RVC). *Mitchell Co.,* Altapass, M (segment 7 only), 11 August 1910, R.V. Chamberlin (RVC). *Buncombe Co.,* Montreat, M, 5 September 1977 (NCSM A1701); Swannanoa, M, 26 May 1923, C.S. Brimley (SNAP) TYPE LOCALITY; 5.2 mi. NW Avery Cr., along NC hwy. 191 at Blue Ridge Parkway nr. French Broad R., M, 1 June 1977, A.L. Braswell (NCSM A1595); Bent Creek Forest Experiment Station, M, F, 30 April 1939, N.B. Causey (ANSP); 8.8 mi. SE Asheville, Lake Powhatan, 2M, 5 September 1977 (NCSM A1706); and 11 mi. S Asheville, along co. rd. 3495, 0.3 mi. E jct. I-26, M, 3F, 16 June 1979 (NCSM A2769). *Polk Co.,* 1.5 mi. NNE Saluda, along co. rd. 1151, 0.3 mi. W jct. co. rd. 1142, M, F, 14 September 1977 (NCSM A1741). *Haywood Co.,* along US hwy. 276 S of Waynesville, M, 24 June 1961, H.V. Weems (FSCA); and 12 miles NW Waynesville, GSMNP, nr. Cataloochee School, 3M, 3F, 8 July 1976 (NCSM A916). *Swain Co.,* 2 mi. NE Bryson City, entrance to GSMNP nr. Deep Cr. Campground, M, F, 16 May 1978 (NCSM A1904). *Transylvania Co.,* 8 mi. NW Brevard, Pink Beds Rec. Area, M, F, 30 July 1958, R.L. and M.S. Hoffman (NMNH); 5 mi. NW Brevard, Sycamore Flats Rec. Area, M, 26 May 1958, L. Hubricht (RLH); between Rosman and Balsam Grove, M, 19 July 1961, R.L. Hoffman (RLH); and Toxaway Gorge SE Lake Toxaway, 3M, 16 July 1961, R.L. Hoffman (RLH). *Jackson Co.,* 4, mi. ESE Cullowhee, along Caney Fk. at John's Cr., M, 23 October 1970, F.A. Coyle (WAS). *Macon Co.,* 1.5 mi. SSE Highlands, Satulah Mtn., M, 4 June 1977, A.L. Braswell (NCSM A1592); Highlands, M, 1 July 1963, A. Douglas (RLH); and Coweeta Hydrologic Station, 2M, 6 July 1978 (NCSM A2318).

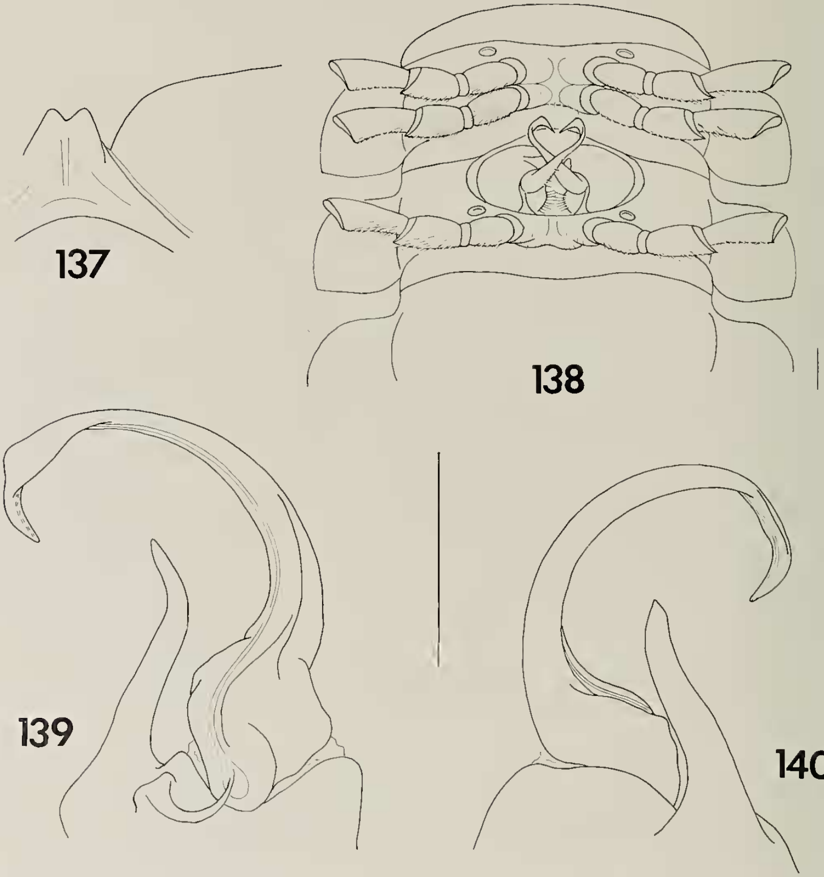
TENNESSEE. — *Cocke Co.,* GSMNP, Cosby Picnic Area, 3M, 8 August 1981 (NCSM A3716). *Sevier Co.,* Gatlinburg, along Ramsey Prong, M, 10 July 1947, H. Hansen (ANSP).

GEORGIA. — *Rabun Co.,* 12 mi ENE Clayton, along GA hwy 28 at W. Fork Chatooga R., M, F, 9 June 1978 (NCSM A2057).

Remarks. — The various forms of *b. brimleii,* which appear dissimilar because of differences in the curvature of the acropodite and the shape of the lateral flange, nevertheless connect through intermediate populations that bridge the gaps in the diagnostic characters of the nominal species reported by Hoffman (1961). In my view, none of the named forms demonstrates enough stability over a large enough area to be retained even at the subspecific level. For example, that previously known as *tela* (Figs.

131-132) has virtually a point distribution, being restricted to the Bent Creek Forest Area of the Pisgah National Forest in Buncombe County. The closest males to this site only vaguely resemble its types, and to retain this name for a single population is impractical.

In August 1981 I collected *b. brimleii* along the creek at Cosby Picnic Area, GSMNP, Tennessee, in precisely the same spots where I discovered *Sigmoria (Sigiria) rubromarginata* in May 1978. The latter was absent in 1981 as was the former on the previous trip. This appears to be a third ex-



Figs. 137-140. *Deltotaria brimelii philia.* 137, process of 4th sternum of male from White Co., GA, caudal view. 138, gonopods *in situ,* ventral view of the same. 139, left gonopod of holotype, medial view. 140, the same, lateral view. Scale line for fig. 138 = 1.00 mm; line for other figs = 1.00 mm for each.

ample of two "sigmoid" species occurring at the same site but having their life histories adjusted so they are prevalent at different times of the year. For *Sigmoria (Cheiropus) australis* and *S. (C.) serrata* in Camden County, Georgia, I (1984a) suggested that this would minimize ecological competition if the species occupied similar niches. Future investigators should therefore determine whether both species occur at Cosby in June or July and whether there is a spring to summer decline in abundance of *S. (S.) rubromarginata* and a concomitant increase in *b. brimleii.*

Deltotaria brimleii philia (Chamberlin), new status Figs. 137-140

Phanoria philia Chamberlin, 1949:101, Fig. 25.
Deltotaria philia: Chamberlin and Hoffman, 1958:30. Hoffman, 1961:34-35, Fig. 3b.

Type specimen. — Male holotype (RVC) collected by W. Ivie, 27 April 1943, at Clarksville, Habersham Co., GA.

Diagnosis. — Coxal apophysis in profile long and slender, extending to near or beyond level of tip of distal zone and well beyond level of prefemur, sides tapering gradually to subacuminate tip; prefemoral process absent or at most vestigial.

Color in Life. — Paranota red or orange, or red on outer margin fading into light orange on inner margin; metaterga black with concolorous stripes, red or orange or reddish on outside and orange on inside, along caudal margins connecting paranotal markings; collum with stripe along anterior margin.

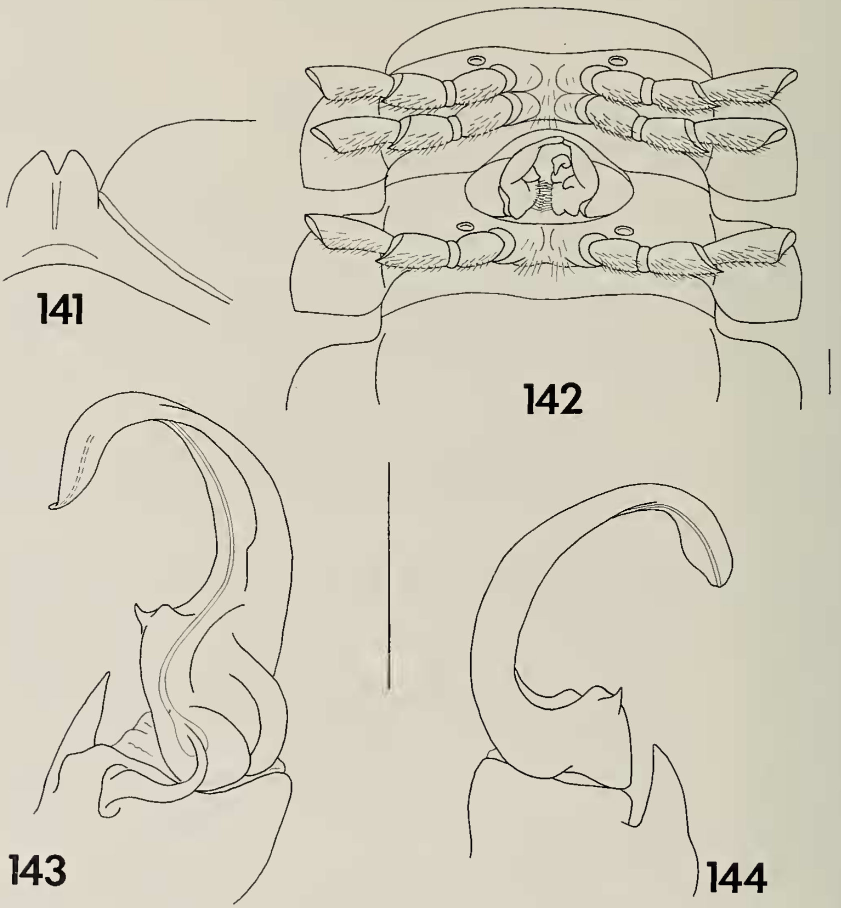
Variation. — The males of *b. philia* agree closely with each other, and I detect no significant variation. Color, however, does vary. The specimens from Graham County, North Carolina, were uniformly orange, while those from the two Georgia locations were red. In South Carolina, the red on the outside of the paranota and stripes grades smoothly into light orange on the inside. These specimens also exhibit a sparkling, metallic sheen that is quite different from the glossy finish on other samples. The South Carolina locality is the most proximal to *lea,* which also displays this sheen, and the inner light orange hues may represent the influence of yellow pigmentation, which is the color found in *lea.*

Distribution. — Southern extremity of the Blue Ridge Province. The race occurs south and west of the nominate subspecies, and the Little Tennessee River appears to be a distributional boundary. Specimens were examined as follows:

NORTH CAROLINA. — *Graham Co.,* 9.5 mi. NNE Robbinsville, along Stecoah Cr. on co. rd. 1236, 0.5 mi. N jct. co. rd. 1235, 5M, 3F, 16 May 1978 (NCSM A1912).

SOUTH CAROLINA. — *Oconee Co.,* 15.5 mi. N Walhalla, Ellicott's Rock Wilderness Area Trail at Fish Hatchery off SC hwy. 107, Sumter Nat. For., M, F, 9 June 1978 (NCSM A2055).

GEORGIA. — *Habersham Co.,* Clarksville, M, 27 April 1943, W. Ivie (RVC) TYPE LOCALITY. *White Co.,* 7.2 mi. E Cleveland, along GA hwy. 255 at Chattahoochee R. and Habersham Co. line, 3M, F, 16 April 1978 (NCSM A1862). *Fannin Co.,* 11.2 mi. S Morganton, Deep Hole Campground off GA hwy. 60, Chattahoochee Nat. For., M, 9 July 1978 (NCSM A2348).



Figs. 141-144. *Deltotaria lea.* 141, process of 4th sternum of holotype, caudal view. 142, gonopods *in situ,* ventral view of male from Gaston Co., NC. 143, left gonopod of holotype, medial view. 144, the same, lateral view. Scale line for fig. 142 = 1.00 mm; line for other figs. = 1.00 mm for each.

Remarks. — Chamberlin (1949) and Hoffman (1961) reported that the acropodite of *b. philia* was apically hastate, but this appearance is actually caused by a profile view of the lateral flange.

Deltotaria brimleii intergrades

Males from the following locality possess coxal processess that extend beyond the level of the prefemoral process and are intermediate in length and shape between the two subspecies. The site is also somewhat intermediate, and I consider the specimens intergrades. Sample data are as follows:

TENNESSEE. — *Sevier Co.,* 7.3 mi. S Gatlinburg, GSMNP, Chimney's Picnic Area, 5M, F, 10 May 1978 (NCSM A1890).

Deltotaria lea Hoffman Figs. 141-144

Deltotaria lea Hoffman, 1961:33-34, Figs. 1c, 3a. Filka and Shelley, 1980:29, Figs. 55-56.

This species was known only from the type locality when it was described and illustrated by Hoffman (1961). Filka and Shelley (1980) added supplemental notes on color, gonopodal variation, and reported a number of localities in North and South Carolina. No new material is available, but the pregonopodal sterna are characterized in more detail, and the gonopods are described in "sigmoid" terminology.

Type specimen. — Male holotype (NMNH) collected by L. Hubricht, 19 April 1956, 4.5 mi. SE Lincolnton, Lincoln Co., NC.

Diagnosis. — Color of paranota and metatergal stripes yellow, with sparkling metallic sheen; coxal apophysis in profile short and triangular, terminating below level of prefemoral process; acropodite distally broad and spatulate; medial flange extending nearly entire length of basal zone, greatly expanded and curved to form concave inner surface of this section; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black with broad yellow stripes along caudal edges connecting paranotal markings; collum with stripe along anterior margin; colors with sparkling, metallic sheen.

Holotype. — Process of 4th sternum moderately long, slightly shorter than widths of adjacent coxae (Fig. 141); 5th sternum with low projections between anterior legs and flattened, elevated areas between 5th; 6th sternum convexly recessed along caudal margin to accommodate apical curvature of acropodites, 7th legs set slightly farther apart than 6th.

Gonopodal aperture ovoid, 3.8 mm wide and 1.4 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 142, not this specimen) with acropodites leaning mediad and apices overlapping in midline of aperture.

Gonopod structure as follows (Figs. 143-144): Coxal apophysis short, narrowly triangular, terminating below level of base of prefemoral process, sides tapering rapidly to acuminate tip. Prefemoral process short, uncinate, directed toward distal zone. Acropodite broad, medial and lateral surfaces expanded through peak (proximal 2/3 of length) into curved laminae, arch high and rounded, overhanging and extending beyond level of prefemoral process; basal zone moderately long and gently curved, inner surface concave; anterior bend broad, poorly defined; continuous through peak with apical curve; peak gently curved, apex at midlength; apical curve broad, poorly defined; distal zone flattened and spatulate, moderately long and directed downward from peak, coplanar with basal zone, flared outward apically; tip subacuminate. Medial flange a broad, curved lamina, located entirely on basal zone, arising proximally and terminating on distal extremity. Lateral flange absent. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Female from Gaston Co., NC. — Length 34.2 mm, maximum width 8.8 mm, W/L ratio 25.7%, depth/width ratio 67.0%. Cyphopods with small receptacle, surface finely granulate. Valves small, equal, surfaces finely granulate.

Variation. — Filka and Shelley (1980) observed that gonopodal variation included the presence or absence of a minute prefemoral process, dimension of the tip of the distal zone, and diameter of the acropodal arch. In rechecking all individuals of *lea,* I find these features to vary randomly throughout the range. The prefemoral process is present on only four individuals: the holotype and one each from Cleveland County, North Carolina, and York and Cherokee counties, South Carolina. Similarly, occasional random males have longer distal zones that extend farther from the peak. All, however, have short coxal processes that terminate below the level of the prefemur and broad medial flanges that extend nearly the entire length of the basal zone.

I also checked for facial setae in males of *lea.* All lack epicranial and interantennal series, about half have frontal setae (1-1), and nearly all have genal setae, usually one per side but occasionally 2-2 or 3-3. Three individuals have a short row of three marginal genal setae continuing from the merged clypeal and labral series.

Ecology. — *Deltotaria lea* occurs in predominantly deciduous woodlands under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — An area about 70 miles long in the Piedmont Plateau of the Carolinas between the Catawba and Broad Rivers, being particularly abundant in the Kings Mountain region on the border of the two states. Localities are detailed in Filka and Shelley (1980).

Remarks. — In addition to color and gonopodal differences, *lea* is also a larger, more robust species than its congener. The paranota project more directly laterad in *lea,* interrupting the slope of the dorsum and imparting a somewhat flattened appearance. In contrast, *brimleii* is more vaulted, and the paranota are more continuous with the slope of the dorsum, extending sharply downward toward the substrate.

Because of its peripheral occurrence in the state, Filka and Shelley (1980) recommended that *lea* be assigned to the Of Special Concern conservation status in North Carolina.

PART III. ECOLOGY

By Rowland M. Shelley

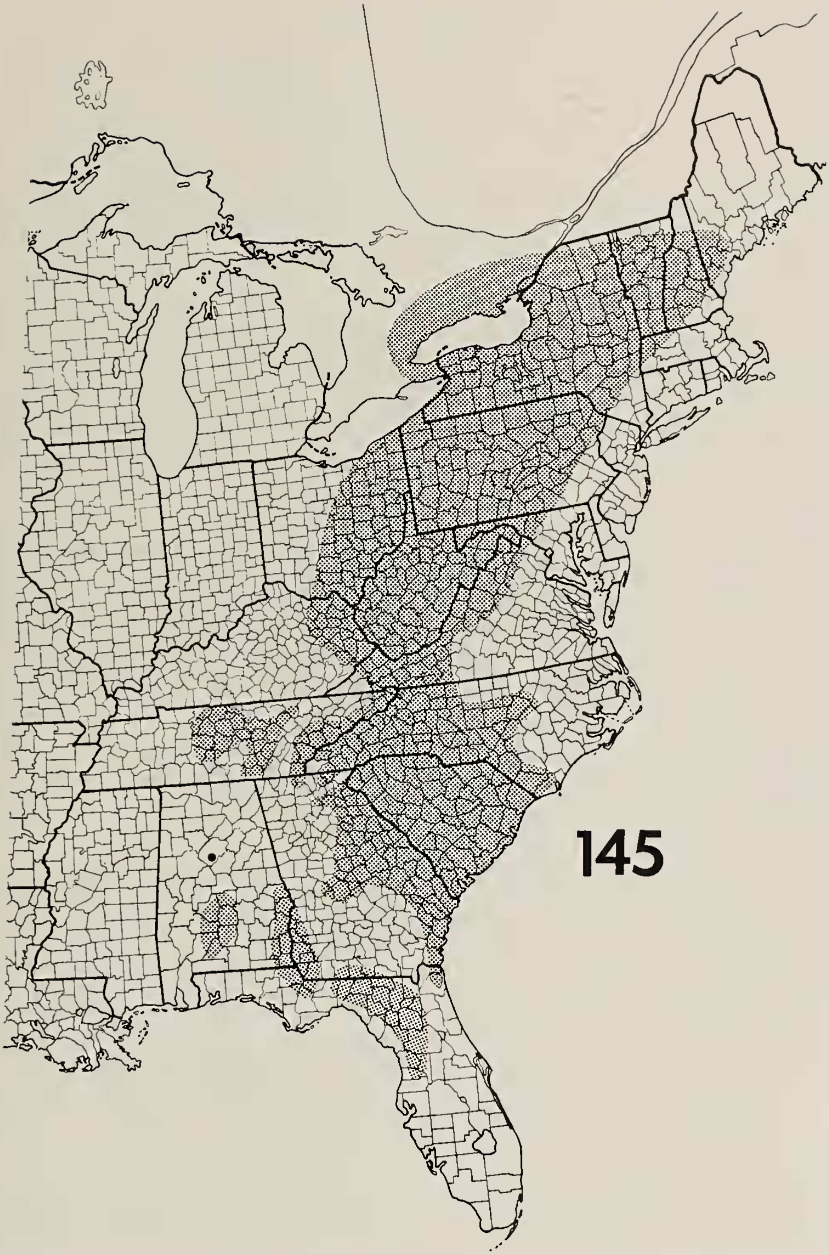
HABITATS. — The characteristics of the cove environments inhabited by species of *Sigmoria s. lat.* were detailed by Shelley (1981a). Theses sites also are preferred by *ainsliei, aphelorioides,* and *prolata (Falloria),* the *haerens* group *(Cheiropus),* the subgenus *Dixioria* (wherever the habitat occurs in the more widely spaced mountains north of the Nolichucky River), and *Deltotaria brimleii.* I have collected the nominate subspecies of *trimaculata (Rudiloria)* in New York and West Virginia, both times in places with cove features. However, it remains to be seen how applicable this habitat is to the subgenus *Rudiloria* as a whole. From what Hoffman (pers. comm.) related about the site where he discovered *whiteheadi (Sigiria),* it also appears to be a cove species and, along with *truncata (Sigiria),* one of only two that can occur in rhododendron litter.

In the piedmont and Atlantic lowlands, *Deltotaria lea,* the subgenus *Cleptoria,* and *persica* of the *planca* group *(Cheiropus)* are found mostly in predominantly hardwood areas under thin layers of leaves on relatively firm substrates near water. This environment also is preferred by the subgenus *Croatania,* although these forms frequently are encountered in predominantly or exclusively pine woods. Farther south and east, *australis, planca,* and *serrata (Cheiropus)* occur in a variety of predominantly hardwood sites, which include the best spots available in the generally unfavorable coastal environments.

West of the Appalachian Mountains, the forms in the Cumberland Plateau and Nashville Basin Provinces of Tennessee occur in a variety of biotopes. Cove environments are widespread in the former, especially north of highway I-40, but surprisingly they are shunned by *picapa (Falloria).* My assistants and I searched in vain for around 40 man-hours in coves near Wartburg, Frozen Head State Park, and other areas in central Morgan County before finally encountering one male and one female in oak woods near the type locality. These were in a different microhabitat, under deep piles of leaves well removed from water. Clearly, *picapa* has ecological preferences different from those of cove dwelling congeners. However, *forficata (Falloria),* occurring north and south of *picapa,* does occur in coves, and the same is true for *abbreviata (Falloria).* Farther south, *houstoni (Falloria)* prefers dry, open areas but still seeks shelter under thin layers of leaves on relatively firm substrates. Cove habitat becomes steadily rarer westward into central Tennessee, and the species of the *mimetica* group *(Falloria)* therefore opt for the best hardwood sites available, with the more secluded and moist ones being preferred. Certain areas of central Tennessee resemble those in piedmont Georgia and South Carolina, and the millipeds likewise are found in the same kind of microhabitats along banks of streams or in moist spots. Exceptional individuals occasionally are encountered in xeric environments, as in Cedars of Lebanon State Park, Wilson County.

SYNTOPY. — I (1981a) previously reported that only one species of *Sigmoria s. lat.* occurs at a given site, and until recently I had not encountered any syntopic apheloriine species, even among different genera. The first instance was the discovery of *australis* and *serrata (Cheiropus)* together in Camden County, Georgia (Shelley 1984a), wherein *australis* was reported as an undescribed species of *Hubroria.* These two species apparently avoid competition by being dominant at different times of the year. The same may be true for *australis* and *Dynoria medialis* Chamberlin at Kolomoki Mounds State Park, Early County, Georgia. A third example may involve *rubromarginata (Sigiria)* and *Deltotaria brimleii* at Cosby Picnic Area, GSMNP, Tennessee. I collected the former there in May 1978 and the latter in exactly the same spots in August 1981, so visits in June and July may yield both. Another example of syntopy came to my attention in July 1984, when Dr. Hoffman sent a male of *whiteheadi (Sigiria)* and one of *l. latior (Sigmoria)* which were taken within a few feet of each other at the type locality of the former. Because *latior* is a ubiquitous species not restricted to cove environments, it does not occupy the same niche as *whiteheadi.* There still are no clear examples of syntopy between cove dwelling congeners, which is in accordance with Gause's theorem that two species cannot indefinitely coexist if they have identical ecological requirements. However, a possible example of syntopy among cove species involves *coronata* and *brooksi (Dixioria)* in Johnson County, Tennessee. More precise knowledge of the habitats of these species is needed before this can be confirmed.

FIG. 145. Distribution of *Sigmoria.* Known discontinuities in the southern half of the main part of the range are shown, but a smooth curve is drawn around the range extremes north of the isthmus in southwestern Virginia. Discontinuities may exist in West Virginia, Ohio, Pennsylvania, and other northern areas, but insufficient sampling has taken place to detect them. The ranges of the groups in the Cumberland Plateau and Nashville Basin of Tennessee, while not known to abut or overlap, are very close and hence are drawn as a single unit. From east to west, the disjunct southern areas correspond to *planca* and populations of *australis,* with one Alabama population of *rileyi* occurring on the northern periphery of the central one. The dot in north-central Alabama corresponds to the Jefferson County record of *rileyi.*



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PART IV. DISTRIBUTION

By Rowland M. Shelley

DISTRIBUTION OF SIGMORIA. — With the inclusion of the new speices and those in the synonymized genera, the distribution of *Sigmoria s. lat.* is enlarged to encompass the shaded areas in figure 145. Overall, the genus ranges from northern New England and southern Ontario to northern peninsular Florida, and from the Atlantic Ocean in South Carolina and Georgia as far west as central Tennessee and central Alabama. A smooth curve is drawn around range extremes in the north, where sampling has been sparse, but known discontinuities are shown from southwestern Virginia southward, where the greatest species diversity occurs and where sampling has been more intensive. The two areas are divided by an isthmus in southwestern Virginia, the northern area being occupied by *Rudiloria* and by one species each of *Dixioria* and *Sigmoria s. str.,* and the southern by the rest of the genus. Physiographically, the main part of the generic range spans the St. Lawrence, Connecticut, Hudson, Delaware, Potomac, Ohio, New, Cape Fear, Yadkin, Catawba, Savannah, Altamaha, and St. Marys Rivers, taking in parts of the New England, Adirondack, Ridge and Valley, Blue Ridge, Piedmont Plateau, and Coastal Plain Provinces.

In central Tennessee, an apparently disjunct area in the Nashville Basin and Cumberland Plateau is occupied by members of the *mimetica, picapa,* and *translineata* groups *(Falloria).* This area is separated from the main one by the Tennessee River and probably represents a real distributional gap. Repeated searches for *Sigmoria* in the northern half of the hiatus in Anderson, Morgan, and Roane counties yielded only *Brachoria.* Farther south, the Tennessee River Valley in Rhea, Meigs, and Bradley counties has been chiefly cleared for pasture or other agricultural uses, and not even *Brachoria* is found there now.

Obvious disjunctions also occur in the extreme south, involving members of the subgenera *Cheiropus* and *Cleptoria.* The most notable gap is the apparent absence of *Sigmoria s. lat.* from most of the southern half of Georgia. Both *australis (Cheiropus)* and *rileyi (Cleptoria)* occur in three disjunct populations, two of which are mostly or completely in Alabama (Figure 68). *Sigmoria (Cheiropus) planca* is the southernmost species and the only one in this area wholly detached from the main generic range.

DISTRIBUTIONS OF SPECIES AND SPECIES GROUPS. — Figure 125 depicts the distributions of *ainsliei, aphelorioides,* and *prolata (Falloria),* and figure 147 shows occurrences within the GSMNP. *Sigmoria aphelorioides* occurs south of the GSMNP and the Little Tennessee River, whereas *ainsliei* is in the Park and the adjacent Ridge and Valley Province. Of the ten "sigmoid" species known from the Park, *rubromarginata*

(Sigiria) is the dominant form in the northern section, north and east of US highway 441. *Deltotaria brimleii* also is abundant, and both species occur as far south as Gatlinburg and the Deep Creek area, on the west and east sides, respectively. South and west of this highway the fauna is dominated by members of the subgenus *Falloria.*

The distributions of species of *Falloria* in the Tennessee disjunct area are shown in figure 126. The *picapa* and *translineata* groups are restricted to the Cumberland Plateau, whereas the *mimetica* group is concentrated in the Nashville Basin but spreads onto the Highland Rim on either side. The sample of *mimetica* from Cheatham County is the westernmost of the genus *Sigmoria.*

The fauna in the lowlands east and south of the Blue Ridge Province is so complex that, for clarity of presentation, it must be shown on two maps (for distributions of the *haerens* and *planca* groups, see Shelley 1982, 1984a). Figure 68 depicts locality records for *australis* and the subgenus *Cleptoria,* and figure 49 shows records for *Croatania.*

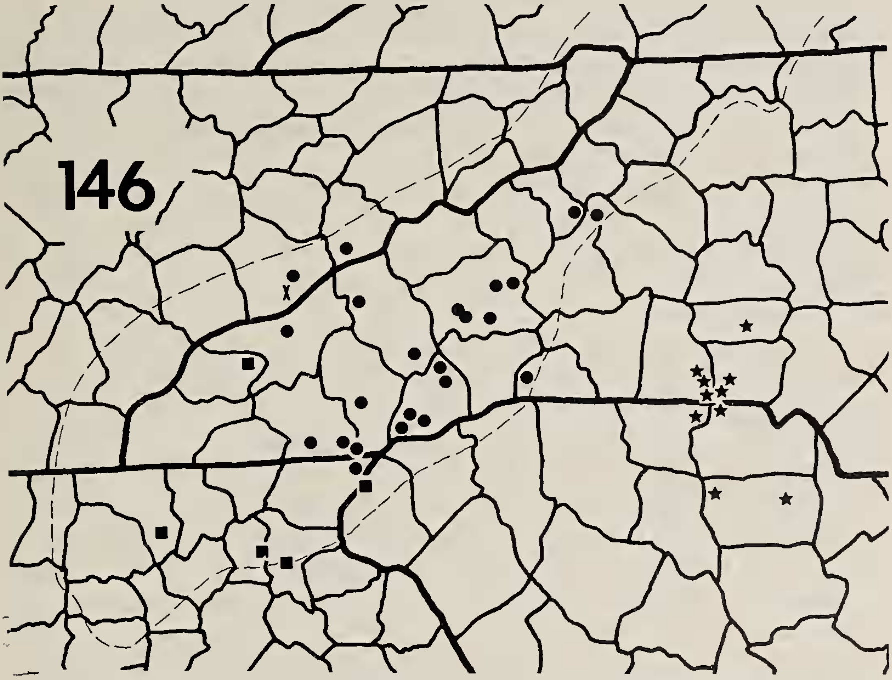

FIG. 146. Distribution of *Deltotaria.* Dots, *b. brimleii;* squares, *b. philia;* X, *brimleii* intergrades; stars, *lea.* The dashed line denotes the approximate boundary of the Blue Ridge Province.

Sigmoria (Cheiropus) australis and *rileyi (Cleptoria)* occur in three disjunct areas. The westernmost sample of *rileyi,* from the southern extremity of the Cumberland Plateau, is some 40 miles north of the closest record of *australis,* in the Fall Zone. *Sigmoria rileyi* also occupies the northern periphery of the Chattahoochee segregate of *australis.* This river bisects the latter area and does not form a distributional limit as it does for *Dynoria medialis* (see Shelley 1984b). The eastern segregate of *australis* hugs the Atlantic Ocean in South Carolina and Georgia, spanning the Savannah, Ogeechee, Altamaha, and Satilla Rivers. It is unknown south of the St. Marys River, but as its distribution in coastal Georgia is similar to that of *serrata, australis* may also occur in northeastern Florida.

Most of the records shown for the subgenus *Cleptoria* in figure 68 are along the Savannah River, where field efforts were concentrated. Although *rileyi* undoubtedly is more widespread, it probably does not occur much farther west because the area around Atlanta has been sampled reasonably thoroughly. In central Georgia the ranges of *rileyi, persica (Cheiropus),* and *Dynoria medialis* are almost exclusive (see Shelley 1984a, b), suggesting that they occupy similar niches. The actual distribution of *bipraesidens* may parallel that of the South Carolina species, *robusta,* in ranging nearly to the Blue Ridge Front. *Sigmoria (Cleptoria) abbotti* hugs the southern side of the Savannah River in both the Piedmont Plateau and the Coastal Plain, but the South Carolina species are limited to the Piedmont south of the Enoree River. The distributions of *shelfordi* and *arcuata* are as stated previously (Shelley 1980a, 1981b), except the Oconee County male is reassigned to the former. *Sigmoria macra* occurs in a band north of these species, and *robusta* occupies a somewhat triangular area in the western tip of South Carolina.

An updated distributional map for the subgenus *Croatania* (Figure 49) includes localities listed in Shelley (1977) and new ones cited herein. The most significant additions are those for *simplex,* formerly known only from the type locality. This site is near the northern range limit, and the species actually extends well past the Fall Zone into the central Coastal Plain. New records for *saluda* extend its range eastward through the Fall Zone to the inner edge of the Coastal Plain. Range additions to *catawba* are minor and areas where it was expected from previous records. *Sigmoria (Croatania) yemassee,* still known only from the two original collections in Jasper and Beaufort counties, and *australis (Cheiropus)* are the only two ''sigmoid'' species in the southern tip of South Carolina, where even *latior* is absent.

The subgenus *Dixioria* (Figure 45) occupies a small area around the contiguous corners of North Carolina, Tennessee, and Virginia, from Tazewell County in Virginia southward to the Nolichucky River. It is known only from the Blue Ridge Province in North Carolina and Tennessee, but in Virginia *coronata* spreads northward into the Ridge and Valley Province. *Sigmoria (Dixioria) coronata, pela, watauga,* and *wrighti* have sharp distributional limits, but only a few records are available for *acuminata* and *brooksi.* Further exploration may expand their boundaries in Tennessee and Virginia; *dactylifera,* however, is restricted to central Ashe County, North Carolina.

Aside from the subgenus *Dixioria,* comparatively little is known about the forms of *Sigmoria s. lat.* occurring north of North Carolina. Vast areas remain to be investigated in West Virginia, Kentucky, Ohio, and Pennsylvania. Available records, plotted in figure 17, reveal clustering of *l. latior (Sigmoria)* and *t. kleinpeteri (Rudiloria)* in southwestern Virginia, the only region to have received much attention. Father north, the plotted ranges of *guyandotta, rigida,* and *mohicana (Rudiloria)* are subject to future expansion; however, the scattered records of *t. trimaculata (Rudiloria)* probably outline its area fairly accurately. The absence of the genus from piedmont Virginia is curious, and the recent discovery of *whiteheadi (Sigiria)* along the escarpment in Patrick County may indicate more surprises in lowlands to the east. Explorations of this area are left to future investigators, and clues to potentially productive environments are available in the ecological accounts here and in Shelley (1977; 1980a; 1981a, b, c; 1984b).

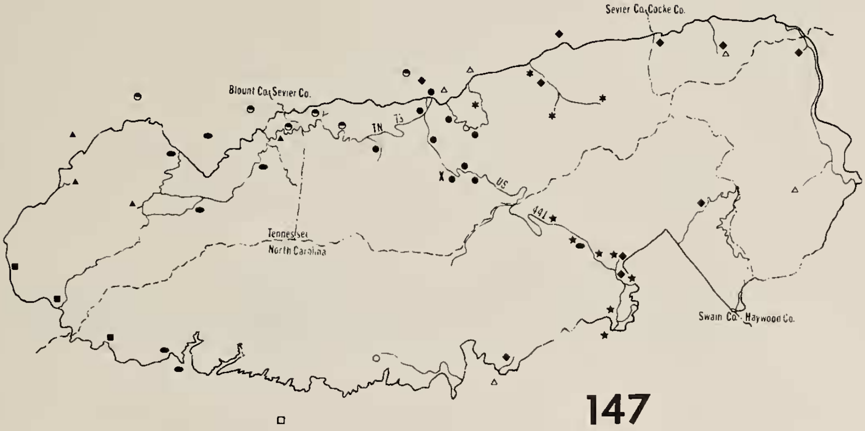

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FIG. 147. Distributions of species of *Deltotaria* and *Sigmoria* in the Great Smoky Mountains National Park and vicinity. Diamonds, *rubromarginata;* stars, *tuberosa;* circle, *nantahalae;* ovals, *translineata;* squares, *lyrea;* solid triangles, *fumimontis;* half-shaded dots, *ainsliei;* dots, *bidens;* asterisks, *prolata;* open triangles, *D. b. brimleii;* open squares, *D. b. philia; X, D. brimleii* intergrades.

TABLE 4. Distribution of Species of *Sigmoria* by Physiographic Provinces

+ Occurrence within the province.
E Endemic to the province.

Taxon	No. (Table 3, Figs. 151-152)	New England Adirondack	Coastal Plain	Piedmont Plateau	Blue Ridge	Ridge & Valley	Appalachian Plateaus	Interior Low Plateaus
trimaculata	1-3	+				+	+	
guyandotta	4						E	
mohicana	5						E	
rigida	6						E	
pela	7				E			
acuminata	8				E			
coronata	9				+	+		
watauga	10				E			
wrighti	11				E			
brooksi	12				E			
dactylifera	13				E			
latior	14-17		+	+	+	+	+	
stenoloba	18			E				
quadrata	19			E				
laticurvosa	20			E				
catawba	21			E				
saluda	22			E				
simplex	23		+	+				
yemassee	24		E					
rileyi	25			+			+	
abbotti	26			E				
bipraesidens	27			E				

robusta	28		E	
arcuata	29		E	
shelfordi	30		E	
macra	31		E	
australis	32	E		
stibarophalla	33			E
divergens	34			E
haerens	35			E
divaricata	36			E
thrinax	37			E
agrestis	38	+	+	
serrata	39	E		
planca	40	E		
persica	41		E	
rubromarginata	42			E
austrimontis	43		+	+
whiteheadi	44			E
triangulata	45			E
nigrimontis	46-49			E
inornata	50			E
truncata	51			E
sigirioides	52			E
areolata	53			E
stenogon	54			E
disjuncta	55		+	+

TABLE 4. Distribution of Species of *Sigmoria* by Physiographic Provinces (Continued)

+ Occurrence within the province.
E Endemic to the province.

Taxon	No. (Table 3, Figs. 151-152)	New England Adirondack	Coastal Plain	Piedmont Plateau	Blue Ridge	Ridge & Valley	Appalachian Plateaus	Interior Low Plateaus
nantahalae	56				E			
leucostriata	57				E			
xerophylla	58				+	+		
aphelorioides	59				E			
translineata	60				E			
fumimontis	61				E			
lyrea	62				E			
ainsliei	63				+	+		
bidens	64				E			
prolata	65				E			
tuberosa	66				E			
forficata	67						E	
houstoni	68						E	
abbreviata	69						E	
picapa	70						E	
mimetica	71							E
pendulata	72							E
crassicurvosa	73							E
Number of Species		1	7	18	35	5	10	3
Percent of Genus		1.5%	10.8%	27.7%	53.8%	7.7%	15.4%	4.6%
Number of Endemic Species		—	4	12	29	—	7	3
Percent of Genus		—	6.2%	18.5%	44.6%	—	10.8%	4.6%

Mostly widely distributed species: *latior (5 provinces); trimaculata* (3 provinces)

PHYSIOGRAPHIC PROVINCES AND ENDEMISM. — Table 4 lists the species of *Sigmoria s. lat.* by physiographic province (Hunt 1967), including also the extent of endemism. Immediately apparent is the preponderance of total taxa and endemics in the Blue Ridge Province, in both cases more than those of the two adjacent regions combined. Slightly over half the total species are represented at least partly in the Blue Ridge, and well over 1/3 of the endemics occur there. The Piedmont and Appalachian Plateaus rank second and third in both categories, and there are no endemics in the Ridge and Valley Province. All three species in the Interior Low Plateaus of central Tennessee are endemic. The southeastern Coastal Plain has four endemics, which are of interest in view of the flat topography and generally unfavorable habitats. Although *disjuncta (Sigiria)* is listed from two provinces, it occurs along the base of the escarpment in South Carolina and Georgia and does not really span the Blue Ridge and Piedmont Plateau regions. In contrast, *simplex (Croatania)* clearly spans the Fall Zone boundary between the Piedmont Plateau and Coastal Plain in South Carolina, inhabiting sizeable portions of both regions. Table 4 also shows the great adaptability of *latior (Sigmoria),* which occurs in five provinces of vastly different environments; the large distribution of *trimaculata (Rudiloria)* does not cover nearly as great a range of biotopes.

DISTRIBUTION OF DELTOTARIA. — The distributions of the species of *Deltotaria* are shown in figure 146. The strict correlation of *brimleii* with the boundaries of the Blue Ridge is clearly evident, although southern populations occur along the edge of the escarpment in Georgia in a manner similar to *S. (Sigiria) disjuncta.* Approximately 55 miles separate the two allopatric species, both of which are sympatric with several species of *Sigmoria s. lat.*

Part IV. Colors and Color Patterns

By Rowland M. Shelley and Donald R. Whitehead

One intriguing aspect of *Sigmoria s. lat.* is the complex variation in color and color pattern. The first observation a collector makes is the color of his specimens, and Table 1 lists the diversity of hues and arrangements. Colors and color patterns tend to be ignored in xystodesmid systematics, but we find their geographic patterns extremely informative.

COLOR PATTERNS. — The three general color patterns cluster geographically as shown in figure 148. The northern 2/3 of the range is mostly comprised of the middorsal spot pattern, which overlaps that of the uniformly black metaterga (paranotal spots only) in southwestern Virginia.

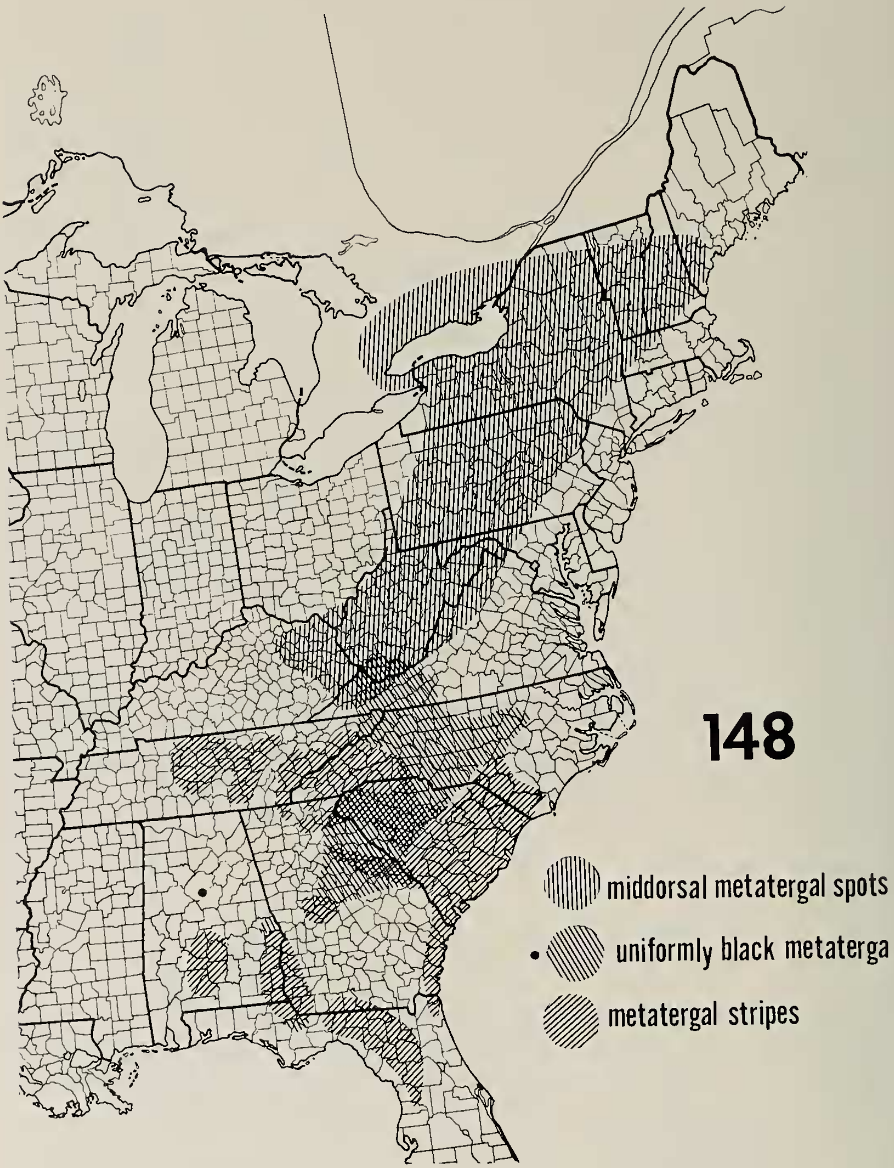

FIG. 148. Approximate distributions of the color patterns of *Sigmoria*.

The latter pattern extends broadly into North Carolina, narrows into South Carolina where it overlaps forms with metatergal stripes, then widens across the Savannah River into piedmont Georgia, where it overlaps a finger of the red stripe pattern and abuts on an isolated population of the latter. The metatergal stripe pattern, occurring in Tennessee and throughout the southern section of the Blue Ridge Province, extends southeastward into South Carolina where it overlaps forms with uniformly black metaterga. The distribution of the striped pattern widens in the Coastal Plain, extending northward back into North Carolina and southward to the southern extremity of the main generic range. Except for the area in northern Alabama and the northern and southern extremities of that bisected by the Chattahoochee River, the striped pattern is also the one found in the southern disjuncts. The peripheral discontinuities in the Chattahoochee segregate represent the southernmost samples of *australis (Cheiropus)* and the Lee County population of *rileyi (Cleptoria)* in the north, both with uniformly black metaterga. The "unstriped" pattern in northern Alabama also reflects *rileyi,* and additional field work is needed to determine the size of the Jefferson County area.

Striped forms omitted from this map include some variants of *t. trimaculata (Rudiloria)* from West Virginia; *whiteheadi (Sigiria)* from Patrick County, Virginia, at the eastern periphery of the uniformly black metatergal pattern; and *mohicana* and *rigida (Rudiloria),* which probably are striped as judged from original descriptions and faded preserved material. Other omissions result from the lack of clear information about the patterns. *Sigmoria (Cleptoria) bipraesidens,* a member of an otherwise unstriped subgenus, is said to be striped (Hoffman 1967) and occurs at the range periphery of the unstriped taxa, but this needs confirmation. The color pattern of *yemassee (Croatania)* is not known, but this coastal species occurs in an area occupied by known striped species and probably also displays this pattern.

With the exceptions noted above, color pattern distribution in *Sigmoria s. lat.* can be generalized as follows: the metatergal spot pattern takes up much of the northern 2/3 of the range, and the uniformly black metaterga and metatergal stripe patterns share rather equally the southern 1/3, the area with the greatest species diversity. In the latter, the unstriped pattern tends to occur in the northern and central parts, and the striped pattern more to the west, east, and south. Sympatry between the latter two patterns is in a relatively broad band, and elsewhere the patterns tend to abut with geographically proximal borders.

COLORS. — The metatergal stripe pattern can be subdivided by colors (Figures 149, 150). As with the general color patterns described above, the colors of the stripes tend to cluster and are not randomly dispersed. For example, blue stripes (Figure 149) tend to occur to the west of red stripes, predominating in central and southeastern Tennessee. Red stripes are found over a much larger area including the southern disjuncts. *Sigmoria (Cheiropus) planca,* the southernmost species, is omitted from figure 149 because its stripes are more orange than red (Shelley 1984a). However, it does bridge the wide red/red hiatus along the Georgia/Florida boundary. Two species of *Falloria* tend to have white or whitish stripes (Figure 150): the northern one, *leucostriata,* has concolorous paranotal spots, whereas the southern one, *nantahalae,* has red paranotal markings. In the central Smokies, the red, white, and blue stripe patterns overlap, the red

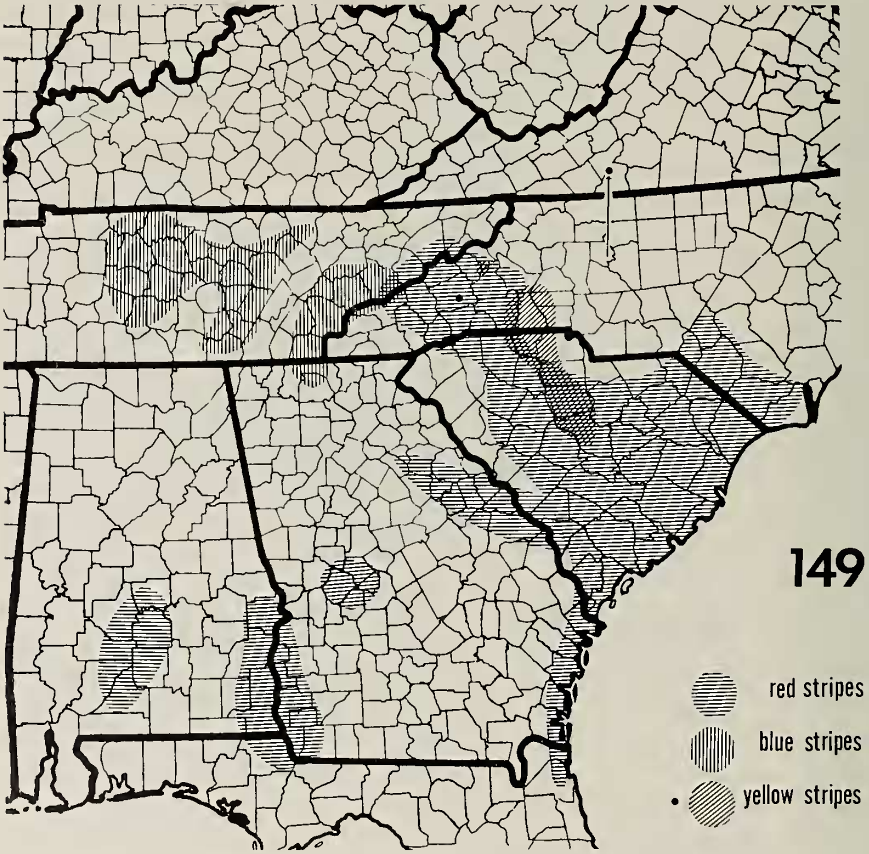

FIG. 149. Approximate distributions of the red, blue, and yellow metatergal stripe colors in *Sigmoria.* The dots in Buncombe County, North Carolina, and Patrick County, Virginia, show isolated locations of yellow stripes in *areolata* and *whiteheadi,* respectively.

represented by *rubromarginata (Sigiria)* and the other two colors by species of the subgenus *Falloria.*

South and east of *nantahalae, disjuncta* and *stenogon (Sigiria)* tend to have concolorous violet or purple paranotal spots and metatergal stripes. The separated distribution shown in figure 150 is somewhat misleading, because intervening populations of *divergens (Cheiropus)* also tend to be dark.

Yellow stripes occur mainly in a band in the Carolinas partly occupied also by red stripes. Small pockets of yellow stripes represented by forms of *Sigiria* are isolated elsewhere in the red stripe area *(areolata, inornata)* and in the uniformly black metatergal area in Virginia *(whiteheadi). Sigmoria (Sigiria) areolata* and *whiteheadi* are known from point distributions and are not known to be polymorphic for color, but *inornata* is polymorphic and may display red, orange, or yellow stripes throughout its range.

IMPORTANCE OF COLOR AND COLOR PATTERN. — Among the eastern Xystodesmidae, most genera of the Rhysodesmini and all genera of the Apheloriini have bold colors on a black background, whereas none of the Nannariini or Pachydesmini display striking contrasts. Some boldly patterned forms apparently are mimetic, as judged from the occurrence of similar colors among sympatric taxa representing distinct lineages. For in-

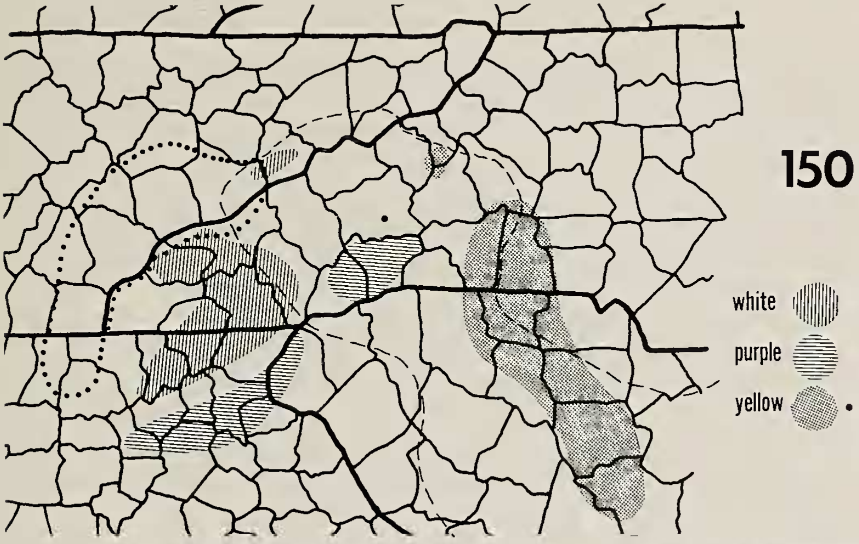

FIG. 150. Approximate distributions of the white, yellow, and violet/purple metatergal stripe colors in *Sigmoria.* The dotted and dashed lines denote boundaries of the blue and red stripes, respectively. The dot in Buncombe County indicates the location of the yellow striped *areolata.*

stance, blue stripes appear in the same geographic areas in both *Brachoria* and *Sigmoria s. lat.*, whereas forms of *Brachoria* in the range of the subgenus *Dixioria* display the yellow paranota/black metaterga of the latter. In other instances, sympatric taxa differ in colors; for example, the red striped *Deltotaria brimleii* overlaps various blue striped species of *Falloria* in the southern Blue Ridge Province. Farther north, however, it is broadly sympatric with the red striped *rubromarginata (Sigiria).*

Geographic distributions of the various colors and patterns considered together with probable instances of convergence suggest informative transformation series useful for phyletic analysis. This information is probably as valuable and as easy to interpret as gonopod structure, and thus equally important in developing a system of relationships within *Sigmoria s. lat.* The combination of color and geography is also useful in field identifications once distributions are well mapped. Some species have distinctive patterns within their areas of distribution, so previously unassignable females may be identifiable if colors and provenance are known. Table 3 facilitates such determinations.

Part VI. Relationships Within Sigmoria

By Donald R. Whitehead and Rowland M. Shelley

In this part, we outline analytical problems encountered in the study, discuss details of the subgenera of *Sigmoria,* resolve subgeneric relationships, and close with a discussion of "mosaic" evolution. We use the term "mosaic" only for observed geographic patterns found in apparently natural groups of primarily allopatric and parapatric species-group taxa which seem to lack cladistic congruence in their various character states. This kind of pattern in millipeds and in other groups of comparatively non-vagile animals resembles a jigsaw puzzle.

Some other terms and notations deserve explanation. Color pattern is usually denoted by a fraction, wherein "red/red" means red paranotal spots and red metatergal stripes, and "yellow/black" indicates yellow paranotal spots and no metatergal stripes. The term "eastern" refers to eastern North America, from the seaboard to the central Great Plains, including the Ozarks. Relationships are depicted by equations; for example, *"Croatania = simplex + (yemassee + (catawba + saluda))"* means that within the subgenus *Croatania, simplex* is sister to the other three species, and *yemassee* is sister to *catawba* plus *saluda.* These cladistic statements, which are exactly analogous to mobiles, are given instead of pictorial trees. Use them with associated maps to visualize implied vicariance patterns.

ANALYTICAL PROBLEMS. — With few exceptions, species diagnostic characters used in *Sigmoria s. lat.* are exclusively in gonopodal structures, and it is difficult to construct satisfactory transformation series. These are complex structures, yet some types of complexities may arise from comparatively simple alterations. Hence, apparently major gonopodal differences may be evidence for nothing more than species level differences. The main somatic features used herein are the relative length of the process of sternum 4 and color patterns. There is no reason to assume convergence in either gonopods or in sternum 4 if derived states of these characters occur in geographically coherent patterns of proximal taxa. We assume the reverse, that geographic coherence represents shared ancestral features. Color patterns must be viewed more critically, not only because of infraspecific variation, but also because we find evidence of mimetic convergence both within *Sigmoria s. lat.* and among related genera. Hence, color patterns also tend to be geographically coherent, but they less convincingly indicate common ancestry.

The genus *Sigmoria* is a cohesive geographic entity (Figure 145) having properties resembling those of a single, rapidly differentiating or fragmenting species. This implies that the history of *Sigmoria* is quite brief, perhaps post-Pleistocene. We infer a continuous, widespread, geographically varied ancestor in rather recent times, which colonized habitats as they became available and subsequently fragmented. Such fragmentation is easy to envision, since most species now occupy specialized cove habitats. Where the allopatric/parapatric mosaic pattern is retained, distributional shifts must reflect ancestral proximity patterns, with range expansion by one segregate achieved only by displacement of another. Present day distribution patterns directly reflect vicariance.

We use the term "incomplete synapomorphy" for a peculiar form of homoplasy occurring in the "mosaic", when the same plesiomorphous and apomorphous states of a character are shared by both members of a sister pair and, by inference, their common ancestor. If characters in the ancestor varied along different geographic gradients, then fragmentation must have cut across character gradients in such a way that derived states of some characters were shared by parts of two or more segregates. Given low vagility in these organisms, there is no reason to assume that the derived character states diffused among the segregates before further fragmentation occurred. These geographically coherent but noncongruent apomorphous character states ("incomplete synapomorphies") suggest common ancestries, but they do not define lineages in diagnostic terms.

Consider what happens when a pepperoni pizza is sliced into wedges, with the pepperoni representing apomorphies. Some pieces of pepperoni will be divided between two adjacent wedges, some slices will have contiguous boundaries, and still other slices will share a point of contact. In *Sigmoria,* the subgenera represent the pie wedges and character state distributions represent the pepperoni. Radial slicing is represented by contact in the southern Blue Ridge by proximal, relatively plesiomorphous members of *Cheiropus, Sigmoria, Sigiria,* and *Falloria.* As the *Sigmoria* pie was sliced by nature, the simplest type of slicing is the most probable. Thus, the first slices should have been cut across the pie rather than in a wedge by wedge sequence.

Ideally, a cladistic hypothesis based solely on morphological character states should be developed for *Sigmoria,* similar to the generic and tribal hypotheses given in chapter VIII. However, the numerous species, combined with apparent convergences, clines, and instances where variation crosses cladistic lines, create a geographic mosaic of reproductive isolates in which the taxonomic or geographic distributions of many character states lack congruence. Our initial attempts at cladistic analyses, which were made without considering geographic distributions, met with failure. We here describe a solution for this mosaic problem, which should apply also to similar problems in other organisms. We consider a character-based cladistic analysis premature at this time. Future investigations should focus on development of other character systems.

Our approach to analysis is based on the observation that the genus seems to have some properties of a single species. We simply test as a null hypothesis the premise that the pieces of the mosaic interlock in a pattern consistent with the properties of a biological species. Hence, the species and subspecies are treated as pieces of a largely two dimensional jigsaw puzzle. Their geographic fit is conspicuous in most instances, thus allowing a search for geographic and character congruence. We did detailed mapping of the species and subspecies taxa, searched for both continuities and major discontinuities in the characters of geographically proximal taxa, and identified as major components (i.e., subgenera) those clusters of taxa that are most strongly discontinuous from proximal taxa.

With one notable exception, *Sigiria,* we are satisfied that our eight allopatric/parapatric subgenera are monophyletic. Remaining is the problem of finding the one (out of 135, 135 possible dichotomous combinations) cladistic arrangement for the subgenera that best fits known facts of geographic and character distributions. The solution, again, is based on a combination of geographic and cladistic inference.

In terms of vicariance partitioning, the subgenera are distributed in a pattern resembling an irregularly cut, eight slice pizza pie. Most slices are adjacent to at least two others, and residual commonality exists in the boundary areas. The pie is sliced but virtually intact — there is little obvious extinction pattern except for gaps between conspecific populations. The slicing pattern itself may be obvious but incomplete. As in the pizza, this might not be noticed until one attempts to isolate the slice.

Maps, figures, and tables both in this paper and in previous papers by Shelley form the basis for character analysis. Out-groups to determine polarity of character states are iterative, and hence polarities may differ among different groups and at different levels.

THE SUBGENERA. — Each subgenus differs in structural diversity, diagnosis, and geography. Thus, some have single species groups, whereas others are more speciose. Some have satisfactory autapomorphies, while others are linked by transformation series or are grouped only by linkage patterns or by "incomplete synapomorphies" which do not apply to all included taxa. Most have only allopatric/parapatric taxa, but others have disjunct and/or sympatric taxa. Except perhaps for *Sigiria,* we think that each subgenus is monophyletic, regardless of its internal composition and despite the lack of complete independence with respect to all structural features. Those features termed "incomplete synapomorphies" at the generic level, here are the opposite; they are plesiomorphies within the subgenus.

We discuss each subgenus in turn, based on a preliminary cladistic hypothesis (Figure 154): genus *Sigmoria* = subgenera *((Rudiloria + Dixioria) + (Sigmoria + (Croatania + Cleptoria))) + Cheiropus + (Sigiria + Falloria).* Undesirable features of this hypothesis are summarized and resolved in our review of subgeneric relationships. Figure 156 is the revised cladistic hypothesis.

Rudiloria. — This subgenus includes only the *trimaculata* group, with five allopatric specific and subspecific taxa *(t. trimaculata,* #1; *t. kleinpeteri,* #2; *trimaculata* intergrades, #3; *guyandotta,* #4; *mohicana,* #5; *rigida,* #6) as mapped in Figure 151, areas 1-6. Detailed distributions are not yet available, and the species and subspecies hypotheses may not survive. The subgenus might even prove to be monotypic. This is the northernmost subgenus, grouped with the partly sympatric, more southern *Dixioria* by apomorphous gonopod orientation. Although divergent in details of gonopodal structure, notably the enlarged prefemoral processes and accessory teeth in *Dixioria,* these two subgenera share other features perhaps indicative of common ancestry.

Aside from sharper acropodal bends in *rigida,* there is resemblance between it and *pela (Dixioria)* (compare Figures 15 and 20), although the range of *ridiga* is separated from that of *Dixioria* by more divergent forms of *Rudiloria.* Both species have acropodites of about the same thickness, and both have a similarly shaped tooth at about the same distance from the tip of the distal zone. We consider this a shared ancestral condition between *Rudiloria* and *Dixioria.* Various features of *rigida* (metatergal stripes; prefemoral process present; acropodite short, not looped, without flanges, with tooth), but not the short process of sternum 4, represent a probable ground plan for *Rudiloria.* The thin, fragile acropodites of various forms of

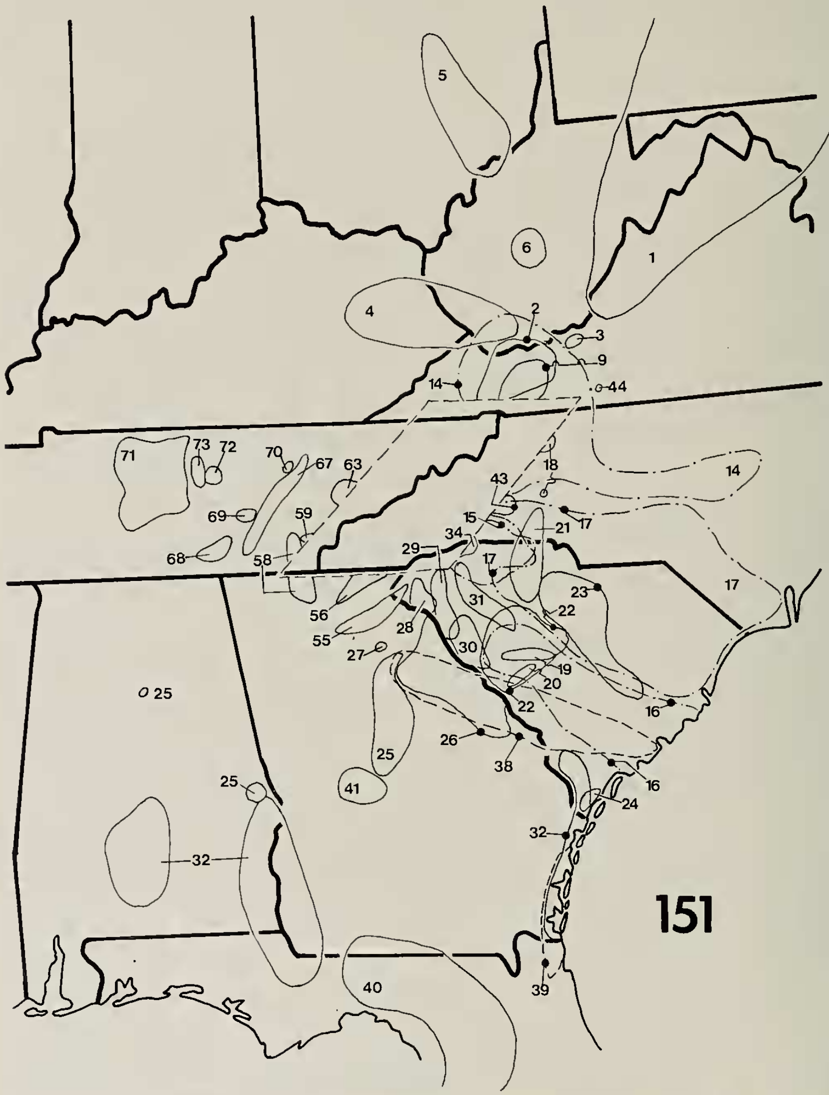

FIG. 151. Generalized species distributions in *Sigmoria;* numbers as in Table 3.

TABLE 5. Apomorphous character states in *Rudiloria*

Character	Taxon						
	1,WV	1	2	3	4	5	6
Acropodite looped	x	x	x	x	—	—	—
lobed	—	—	x	—	x	—	—
bent	—	—	—	—	—	x	xx
not toothed	x	x	x	x	x	x	—
Prefemoral process absent	—	—	—	—	x	x	—
Process of sternum 4 short	—	—	—	—	x	x	x
Metatergal spots (not stripes)	—	x	x	x	x	—	—

Taxa numbered as in Table 3: WV indicates West Virginia samples. Character states range from plesiomorphous (—) to most apomorphous (xx).

Rudiloria and *Dixioria* are perhaps convergent in this respect with those of such taxa as *sigirioides* (which is geographically proximal to *pela*), *stenogon,* and *triangulata (Sigiria).*

Some characteristics of members of *Rudiloria* are summarized in table 5. Presence of dorsal metatergal spots rather than stripes in *guyandotta, t. kleinpeteri, trimaculata* intergrades, and all but a few western *t. trimaculata* is unique within the genus. This color pattern may reflect relationship with *Dixioria* in which neither dorsal spots nor stripes are present. However, since the two subgenera are partly sympatric, the color pattern might represent mimetic convergence. The process of sternum 4 is moderately long in both subspecies of *trimaculata,* an ancestral condition shared with most members of *Dixioria.* These two subspecies also differ from other *Rudiloria,* as well as from *Dixioria,* in having a strongly looped acropodite, a derived state. Two species, *guyandotta* and *mohicana,* lack a prefemoral process, another derived state.

In the nominate subspecies of *trimaculata* the looped acropodite tapers smoothly and continuously to the tip, whereas *t. kleinpeteri* has expansions or lobes at the lowest point in the loop or midlength of the distal zone. In West Virginia, adjacent to the latter's range, is *guyandotta,* in which the distal zone is expanded and extends a short distance below the peak. The lamella is smaller than the lobes of *t. kleinpeteri* but has the same general contours, and *guyandotta* may be merely a form of the latter with the distal zone shortened and the lobes reduced. However, the transition is sudden, with no intermediate forms such as occur between the two subspecies of *trimaculata,* and *guyandotta* also lacks the prefemoral process found in *trimaculata.* In Ohio, *mohicana* has nearly the same acropodal configuration as *guyandotta* but with slightly sharper angles and without the distal zone expansion. In West Virginia, *rigida* has basically the same acropodite as *mohicana* but with still sharper bends, and it also has a tooth and a prefemoral process.

Thus, there is a circular gradient from a looped acropodite without lobes or expansions (and with a prefemoral process), to one with flanges, to a shorter, non-looped one with flanges (and without a prefemoral process), to a short one with slight angles and without flanges, to a short one with strong angles (and with a tooth and a prefemoral process). Between *t. trimaculata* and *t. kleinpeteri* the character change is bridged by intermediates, whereas between *t. kleinpeteri* and *guyandotta* it is abrupt. More collecting is needed in Kentucky, West Virginia, and Ohio to determine the nature of other transitions. The acropodal configuration in *mohicana* could connect directly with that in *t. trimaculata,* and the possibility of a clinal continuum is enhanced by the fact that West Virginia samples of *t. trimaculata* agree with *mohicana* in having metatergal stripes rather than dorsal spots. Just as the acropodite of *guyandotta* may be shortened from that of *t. kleinpeteri,* the structure in *mohicana* may be a reduction of that of *t. trimaculata.*

The looped acropodites of *trimaculata* are convergent with those of *ainsliei* and *aphelorioides (Falloria),* approximately 125 miles to the south, and with *Apheloria,* whose range overlaps all three species. Other aspects of the acropodites of these forms do not exhibit such similarities.

Dixioria. — This subgenus includes only the *pela* group, with seven closely spaced species taxa as mapped in figures 151-152, areas 7-13. These taxa share a distinctive body form, and they share with *Rudiloria* a distinctive gonopod orientation.

The distribution of *Dixioria* overlaps that of *Rudiloria,* is adjacent to that of *Sigiria,* is overlaid by that of the ecological generalist *latior (Sigmoria),* and is separated by a small gap (ca. 45 miles) from that of *Croatania. Dixioria* and *Rudiloria* share with *Sigmoria s. str., Croatania,* and *Cleptoria* some non-gonopodal features, including the tendencies to lack metatergal stripes and to have relatively long processes on sternum 4. Furthermore, the enlarged prefemoral processes of *Dixioria* and the more southern *Croatania* occur in close geographic proximity. An alternative relationship *(Rudiloria, Dixioria, Sigmoria s. str., Sigiria, and Falloria)* is suggested by geographic proximity of forms having relatively delicate acropodites. However, as we show later in this chapter, we now regard *Dixioria* and *Rudiloria* as a lineage sister to the rest of the genus.

The most differentiated member of the *pela* group is *dactylifera* (#13), which has the process of sternum 4 short (a derived state) and lacks an accessory tooth (polarity undetermined). If lack of an accessory tooth is ancestral, *dactylifera* is sister to the rest of the *pela* group. Otherwise, it might be a derived element.

In *Dixioria* the species are mostly parapatric with abrupt transitions, a prime reason for considering them reproductively isolated along with the apparent syntopy between *brooksi* (#12) and *coronata* (#9) in Tennessee. More sampling is needed in the transition areas between the forms in this state and Virginia to determine if changes occur as abruptly as in the heavily sampled areas in North Carolina.

A trend towards a longer tooth and a longer distal zone from *coronata* (#9) to *wrighti* (#10) occurs in steps involving the geographically intermediate *watauga* (#11), which has an apomorphous, more distal accessory tooth. Thus, a clinal continuity in one respect is matched by a discontinuity in another, and recognition of *watauga* as a separate species is the most conservative action consistent with the present knowledge. *Dixioria* may actually contain as few as three species, and we treat it as a superspecies in which a detailed cladistic hypothesis is unwarranted.

Sigmoria. — This subgenus (Figures 151-152, areas 14-20) includes the *quadrata* group with two adjacent piedmont species (*quadrata,* #19, and *laticurvosa,* #20) and the *latior* group with two ecologically differentiated species (the widespread, polytypic *latior,* #14-17, and the bipopulational *stenoloba,* #18). The two groups are associated by the flange on the peak of

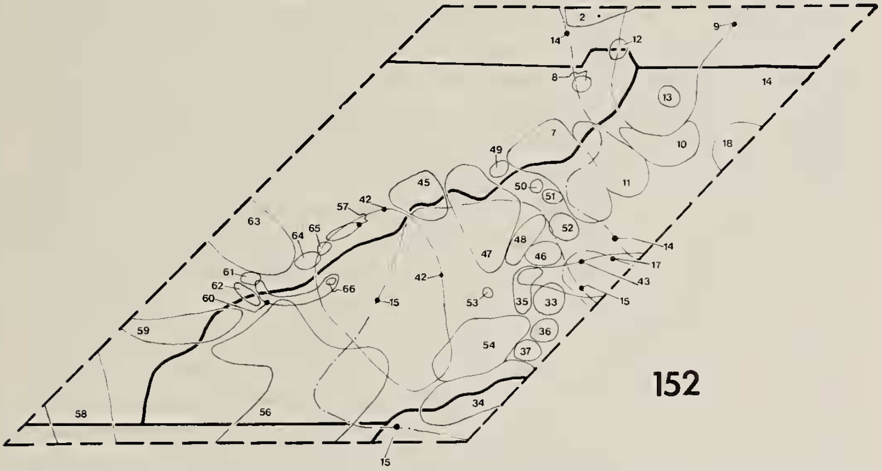

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FIG. 152. Generalized distributions of *Sigmoria* species in the southern Blue Ridge Province; numbers as in Table 3.

the acropodite and by geography: *Sigmoria* = *(latior* + *stenoloba)* + *(quadrata* + *laticurvosa).*

A clear and convincing pattern of geographic races and intergrades is evident in *latior,* far more so than elsewhere in the genus wherein fragmentation patterns are more complete. With its broad ecological tolerances, *latior* is able to spread between localities and is found moving on the substrate more often than any congener. The ecologically generalist nature of *latior* may represent an ancestral feature, if the ancestor of the genus was widespread and geographically varied.

Sigmoria (Sigmoria) latior overlays the ranges of numerous other taxa. Its distribution clarifies the relationship between the *quadrata* and *latior* groups, which otherwise would be disjunctive. It also helps explain the curious, disrupted range of *stenoloba,* which lacks metatergal stripes. If this condition were viewed as synapomorphous, the only possible ancestor for *stenoloba* would be *l. latior;* thus, a species would be derived from a sympatric subspecies. However, lack of metatergal stripes in *l. latior* and *stenoloba* is shared with various members of *Rudiloria, Dixioria, Croatania,* and *Cleptoria.* Also, the gonopodal flanges of *latior (s. lat.)* are more developed than those of *stenoloba,* an apomorphic condition arguing against shared ancestry between *l. latior* and *stenoloba.* Hence, we accept a sister relationship between *latior (s. lat.)* and *stenoloba,* with the disrupted range of the latter resulting from displacement by the more successful *latior* (Shelley 1981a). *Sigmoria (Sigmoria) stenoloba* is known from Wilkes and Catawba counties, North Carolina, its two allopatric populations separated by about 40 miles and distinguished only by minor gonopodal differences.

Certain taxa of *Sigiria* (notably, *whiteheadi, areolata,* and some individuals of *inornata)* have yellow paranotal spots and yellow metatergal stripes as occur in some populations of *l. munda (Sigmoria),* but they otherwise most closely resemble various red/red forms of *Sigiria.* We consider yellow/yellow as an ''incomplete synapomorphy'', given a probable transformation series of red/red to yellow/yellow to yellow/black, because red/red and yellow/yellow occur in both *Sigmoria s. lat.* and *Sigiria.* Mimetic convergence is unlikely. For example, *whiteheadi* structurally fits best with *austrimontis (Sigiria)* but is syntopic with yellow/black *l. latior.* It seems to share a distant common ancestry with *latior (s. lat.)* but to have retained an intermediate, ancestral yellow/yellow coloration. It might seem to represent a range extrusion from *austrimontis* which failed to achieve the *l. latior* color pattern, but a range extrusion is incompatible both with a simple fragmentation pattern and with the major range disjunction between *austrimontis* and *whiteheadi.* The disjunctive *whiteheadi* represents a remnant of an ancestral yellow/yellow continuum.

Both members of the *quadrata* group occur within the range of *saluda (Croatania).* This is one of rather few examples of secondary sympatry among ecologically restricted species. Both species of the *quadrata* group have metatergal stripes, and we infer that their ancestry was to the southeast of the range of the ancestral component which lacked stripes. The more widespread *saluda* is thus the incursive element. If the ancestry of the *quadrata* group was to the southeast of that of *Croatania,* then the subgenus *Sigmoria* itself was ancestrally eastern.

The subgenus *Sigmoria* is characterized by the reflexed acropodite tip, a feature also found in some samples of *arcuata,* which we think is a sister element within *Cleptoria* and which therefore might represent ancestral conditions found in *Cleptoria* and *Croatania.* However, a reflexed tip also is found in *stenogon (Sigiria)* and *fumimontis* and *aphelorioides (Falloria).*

Aside from the lack of metatergal stripes in some members of the *latior* group as well as in various species of *Cleptoria* and *Croatania,* a relatively long process of sternum 4 occurs in the latter two subgenera and in the *quadrata* group. Both conditions are "incomplete synapomorphies", homoplasious with respect to one another and to various gonopodal features yet geographically coherent.

Sigmoria (s. str.) is a discrete component of *Sigmoria (s. lat.),* but it is less clear how it relates to other subgenera. It appears to be a geographic subdivision with residual connections to other proximal subgenera along what are now disconnected clinal gradients. Geographic considerations and a general similarity of gonopods with those of *arcuata (Cleptoria)* seem to suggest a relationship of *Sigmoria s. str.* with *Croatania* and *Cleptoria* (see figure 154). In turn these subgenera might seem related to *Rudiloria* and *Dixioria* because of the presence in some members of a relatively long process on sternum 4 or the absence of metatergal stripes. However, there also are gonopodal similarities between species of *Sigmoria s. str.* and certain species of *Sigiria* and *Cheiropus* (notably *areolata* and *stibarophalla,* previously assigned to the *latior* group by Shelley 1981a). For reasons developed later in the chapter, we now consider *Sigmoria s. str.* to share common ancestry with *Sigiria* and *Falloria* (see Figure 156).

Croatania. — This subgenus contains only the *catawba* group, with four species taxa (Figure 151, areas 21-24). *Croatania* has an autapomorphy, the irregularly notched expansion of the basal zone. Possibly also autapomorphous, though shared with the more northern *Dixioria,* is the large prefemoral process. The spine on the basal zone in some but not all *Cleptoria* is considered homologous with the enlarged basal projection on the notched expansion of *Croatania.* This, in combination with the generally robust gonopods of both subgenera, specifies sister relationship. "Incomplete synapomorphies" in color and the form of the process of sternum 4 seem to link *Croatania* and *Cleptoria* with *Sigmoria, Dixioria,* and *Rudiloria,* but we provide a more satisfactory set of subgeneric relationships later in the chapter.

Relationships within *Croatania* are clear. In *simplex* (#23), the process of sternum 4 is apomorphous in being short rather than long, and in *catawba* (#21), *saluda* (#22), and *yemassee* (#24) the prefemoral process is apomorphous in being more greatly enlarged. This represents an obvious east/west vicariance. Over 100 miles downstream in the Savannah River Valley, *yemassee* differs from the other taxa in having smaller teeth in the expansion and a decidedly more proximal medial flange, which occurs on the distal extremity of the basal zone. This represents a second, south/north vicariance. In summary, *Croatania = simplex + (yemassee + (catawba + saluda)).*

This simplicity is confused by the geographic distribution of color patterns. The northernmost taxon, *catawba,* is yellow/black, as are proximal populations of *simplex.* Farther south, approaching the range of primarily red/black *Cleptoria, saluda* and central populations of *simplex* also are red/black. Farther east, populations of *simplex* in the Fall Zone and Coastal Plain are red/red, and we predict that *yemassee* also is red/red as are all coastal congeners. Color patterns are not uniformly distributed by taxa, but they do form geographically coherent distributions. In some instances, they might be explained by mimetic convergence, but this explanation should apply only to sympatric taxa, not to such parapatric taxa as the geographically proximal species of *Cleptoria* and *Croatania.* Herein lies the basis for interpreting the color combination yellow/black or red/black as an "incomplete synapomorphy": its geographic distribution links various allopatric but geographically proximal taxa of these subgenera with *Sigmoria* and *Dixioria.* Where a similar color combination is found elsewhere, as in the southernmost population of *australis (Cheiropus),* it evidently is disconnected and may be a random convergence.

Shelley (1977) proposed dispersal hypotheses to account for distributions of species of *Croatania,* but they are inappropriate because the animals are not sufficiently vagile. Although the species inhabit a greater diversity of biotopes than those of the proximal or sympatric *rileyi (Cleptoria)* and *quadrata (Sigmoria)* groups, their habitat requirements are still too narrow to allow them to spread through an area with so many biotopes.

Cleptoria. — This subgenus contains only the *rileyi* group (Figure 151: *rileyi,* 25; *abbotti,* 26; *bipraesidens,* 27; *robusta,* 28; *arcuata,* 29; *shelfordi,* 30; *macra,* 31). Various differently distributed "incomplete synapomorphies", including a "bird's head" acropodite and/or presence of a basal spine, confirm monophyly. The basal spine is homologous to the enlarged basal projection on the notched expansion in proximal taxa of *Croatania,* hence these subgenera are sister groups. Puzzles within the *rileyi* group include the resemblance of *arcuata* in some gonopodal features to *Sigmoria s. str.,* the complex distributions and variations of *macra* and *shelfordi,* and the disjunctive populations of *rileyi* and *shelfordi.*

Sigmoria (Cleptoria) arcuata is sister to the rest of the group, having a relatively slender acropodite, a laminate rather than thickened lateral flange, no distal lobe (''bird's head''), and, in the southernmost population (in Abbeville County, South Carolina), a reflexed tip (see table 6). Whether these conditions are ancestral or secondary is unclear, but they suggest features found in *Sigmoria s. str.* and perhaps represent other instances of ''incomplete synapomorphy''. Presence of the basal spine confirms placement of *arcuata* in *Cleptoria.* There is obvious circular reasoning in the postulate that gonopods are ancestrally stocky in *Croatania/Cleptoria,* if the relatively slender gonopods of *arcuata* are used to suggest a still more distant common ancestry with *Sigmoria.* Once again, ''incomplete synapomorphy'' provides a geographically plausible explanation.

A curious puzzle is the isolated western, apparently relictual population of *shelfordi,* which is separated from the main range of the species by *arcuata* and which lies adjacent to the range of *robusta.* This form lacks the prefemoral process, perhaps an ancestral ''incomplete synapomorphy'' shared with *arcuata.* We believe that the absence of a prefemoral process in *rileyi* and *bipraesidens* represents convergence with *arcuata* and the western form of *shelfordi,* because of the disrupted geographic distribution of this character state. Proximal populations of *shelfordi* and *macra* resemble one another, and although there are no clear intergrades, the taxa may even be conspecific. The proximal populations, the easternmost of *shelfordi* and southernmost of *macra,* tend to have a spur on the peak of the acropodite, and the former also tends to lack the basal spine as does *macra* throughout its range. Thus, although there is no synapomorphy for *shelfordi* and *macra,* the ''incomplete synapomorphies'' link them as sister species. Together, they are sister to the remaining four species, which are grouped by an upward shift of the medial flange from the basal zone toward the peak. The presence of the isolated western population of *shelfordi* is accordingly explained by vicariance partitioning: *arcuata* separated first; *shelfordi + macra* separated next, in an arcuate band to the south of *arcuata;* then, the range of *shelfordi* became subdivided. Next, *robusta* became isolated, as the ''bird's head'' became more sinuate in the southern taxa. Later, the medial flange shifted still farther onto the peak and the prefemoral processes were lost in *rileyi* and *bipraesidens.* Thus, the cladistic

Table 6. Apomorphous character states in *Cleptoria*

Character	Taxon									
	25	27	26	28	31n	31s	30e	30w	30W	29
Acropodite massive	xx	xx	xx	xx	xx	xx	x	x	x	—
thickened, not laminate	xx	xx	xx	xx	xx	xx	x	x	x	—
"bird's head"	xxx	xxx	xxx	xx	xx	xx	x	x	x	—
medial flange on peak	xx	xx	x	x	—	—	—	—	—	—
with spur on peak	—	—	—	—	—	x	x	—	—	—
without basal spine	—	x	—	—	x	x	x	—	—	—
Prefemoral process absent	x	x	—	—	—	—	—	—	x	x
Without metatergal stripes	—	x	—	—	—	—	—	—	—	—

Taxa numbered as in Table 3, with letters to indicate north, south, east, or west populations; W represents the isolated population of *shelfordi*. Character states range from plesiomorphous (—) to most apomorphous (xxx).

hypothesis: *Cleptoria* = *arcuata* + ((*shelfordi* + *macra*) + (*robusta* + (*abbotti* + (*rileyi* + *bipraesidens*)))).

Except for *bipraesidens*, the color pattern of *Cleptoria* is red/black. In this peripheral species, however, it reputedly is red/red (Hoffman 1967). The disjunct Chattahoochee population of *rileyi* lies just north of red/red forms of *australis (Cheiropus)*, in which the southernmost population also is red/black. Thus, there may be two disjunctions here, that in *rileyi* and that in the red/black pattern. If the latter disjunction exists it may be a relict of a once more widespread distribution of this character state, but it might also be convergent.

The disjunct populations of *rileyi* represent one of three instances in *Sigmoria s. lat.* of non-divergence among conspecific allopatric populations; the others obtain in *australis (Cheiropus)* and *stenoloba (Sigmoria)*. The main population of *rileyi* is in piedmont Georgia, and satellite populations occur about 100 and 200 miles west in Lee and Jefferson counties, Alabama. Hoffman (1967) considered that in Lee County to be a distinct geographic race and predicted eventual discovery of material in the gap. However, the hiatus has been explored reasonably thoroughly at the time of year known populations are extant, and the gap appears to be real. Gonopods of all populations are practically identical, and subspecific status is unwarranted.

The acropodites of *rileyi, abbotti, bipraesidens,* and *robusta* in Georgia and South Carolina are massive and heavily sclerotized, and in this respect they are convergent with those of *crassicurvosa* and *pendulata (Falloria)* in central Tennessee. Individuals of the latter species even display thick subterminal acropodal lobes similar to those on the outer surfaces of the peaks and distal zones in *rileyi* and *abbotti.* The lobes are not homologous, however, as those in *rileyi* and *abbotti* represent modified lateral flanges, and the ones in the Tennessee species are extraneous and located on the medial surfaces. *Sigmoria (Falloria) fumimontis,* in the Great Smoky Mountains of eastern Tennessee, also has a heavy acropodite but the general configuration is more reminiscent of *latior (Sigmoria).* This also is convergence, because the narrow medial flanges, medial tilting of the peak, and divided prefemoral process clearly assign *fumimontis* to the *translineata* group *(Falloria).*

Hoffman (1967) and Whitehead (1972) proposed dispersal hypotheses to account for distributions of species of *Cleptoria,* but as with *Croatania* they are inappropriate because the animals are insufficiently vagile. These hypotheses did not account for *shelfordi, arcuata,* and *robusta,* but they incorrectly included *divergens (Cheiropus).*

Cheiropus. — This major component does not form a neat, definable group and is difficult to relate to the other subgenera. However, an undeniable transformation series links *stibarophalla* to the progressively more derived taxa formerly assigned to the separate genera *Prionogonus* and *Cheiropus* (Shelley 1982, 1984a), and the overall distribution of the subgenus provides an explanation for the relationships and distribution of *australis.* Both distributions and characters of the *planca* group, formerly the sole constituent of the genus *Cheiropus* (Shelley 1984a), seem superimposed upon rather than part of the generic mosaic, and our interpretations may need perceptive scrutiny in the future. We recognize ten species arrayed among the *australis* (#32), *divergens* (#33-34), *haerens* (#35-37), and *planca* (#38-41) species groups: *Cheiropus = australis + (divergens + (haerens + planca))* groups, mapped in figure 151.

The monobasic *australis* group has one of the three species in the genus with disjunct populations — one in coastal South Carolina and Georgia, one in south-central Alabama, and an intermediate one spanning the Chattahoochee River in southwestern Georgia, southeastern Alabama, and adjacent Florida. The latter two populations are approximately 40 miles apart and may prove to be connected, although appropriate habitats have been investigated without success. However, the central and eastern populations are so far apart as to virtually preclude extant linkage. Gonopods in all three areas vary within the same limits, and the populations are clearly conspecific. The only curious character anomaly is in color pattern, with extreme southern representatives of the central population red/black rather than red/red.

Superficially, *australis* most resembles *stibarophalla,* at the opposite range extreme of *Cheiropus.* If *australis* is sister to the rest of the subgenus, this similarity may be explained as ancestral, and so may be the geographic separation of the similar elements. Moreover, an explanation for the disjunct populations arises from the same reasoning. They once were connected in the north and subsequently displaced by other forms of *Cheiropus* and/or *Cleptoria.* However, there is no good synapomorphy for the sister lineage, unless comparatively massive gonopods in *stibarophalla* and *divergens* is so considered. We adopt this scenario for explanatory purposes and erect a separate species group for *australis.*

The next vicariance in *Cheiropus* occurred in the north, separating the conservative *divergens* group *(stibarophalla,* #33, and *divergens,* #34) from those that developed acropodal solenomerites. Again, there is no precise autapomorphy for the *divergens* group, formed for vicariance reasons. If *stibarophalla* is the conservative gonopodal type from which other *Cheiropus* arose, geographic connections to them make sense only if *stibarophalla* and *divergens* shared common ancestry because of the relative geographic position of *stibarophalla.* Otherwise, the range of *divergens* represents a discontinuity between those of the *haerens* and *planca* groups.

One interesting feature of the *divergens* group is that the species *divergens* separates the ranges of *stenogon* and *disjuncta (Sigiria),* and proximal populations of all three taxa tend to be dark or purplish in markings. These are the only congeners so marked, and we consider this still another example of ''incomplete synapomorphy''. Mimetic convergence is unlikely, since the ranges of the three taxa are allopatric rather than sympatric. The gonopods of *divergens* are sufficiently unlike those of the other two species to suggest close relationship.

The *haerens* group *(Prionogonus sensu* Shelley 1982) has a relatively feebly developed solenomerite intermediate between the absence of such a structure in the *divergens* group and the well developed one in the *planca* group. It also is defined by the autapomorphous row of spurs on the outer surface of the basal zone. This feature is unique among xystodesmids and not homologous to modifications of this region in the *tuberosa (Falloria), rileyi (Cleptoria),* and *catawba (Croatania)* groups. The species geographically most proximal to the *planca* group is *thrinax,* which in general gonopodal form also is structurally most similar to the most proximal member of the *planca* group, *agrestis.* The *haerens* group includes three parapatric species *(haerens,* #35; *divaricata,* #36; and *thrinax,* #37) with small geographic ranges, and, like the *australis* and *divergens* groups, it is part of the cohesive generic mosaic.

The *planca* group *(Cheiropus sensu* Shelley 1984a) includes four allopatric, more or less disjunct species so strongly differentiated from one another that three generic names have been associated with them. However, they lack obviously "sigmoid" gonopods, clearly an apomorphic condition. Also, an overall west to east clinal trend toward increased acropodal serration which persists independent of speciation is manifested in proximal populations of *agrestis* (#38), *serrata* (#39) and *planca* (#40) (Shelley 1984a). Moreover, *planca* is structurally intermediate between *serrata* and *persica* (#41). Thus the *planca* group = *agrestis* + *(serrata* + *(planca* + *persica)).*

This species group weakens our generic hypothesis for *Sigmoria.* Not only is it differentiated by having secondarily curvilinear rather than "sigmoid" gonopods, but its distribution broadly overlaps that of various other southern members of the genus. Sympatry occurs within *Cheiropus* itself, between *serrata* and the syntopic eastern population of *australis,* and also between *agrestis* and two species of *Cleptoria.*

Sigiria. — This subgenus (Figures 151-152, areas 42-55) has two major subunits which are geographically contiguous but structurally disconnected by divergent forms, the *rubromarginata* (#42-52) and the *stenogon* (#53-55) species groups.

The *stenogon* group includes three geographically associated species, *stenogon* (#54), *areolata* (#53), and *disjuncta* (#55). Of these, *disjuncta* is anatomically similar to *nigrimontis* (#46-49) and formerly was grouped with it (Shelley 1981a). However, the course of the prostatic groove differs, the color is purple/purple as in the most proximal populations of *stenogon,* and its range is separated from that of *nigrimontis* by *stenogon* and *areolata,* and species of the *rubromarginata* group. The adjacent species *areolata* and *stenogon* diverge in gonopodal features from *disjuncta.* Thus, the *stenogon* group = *disjuncta* + *(stenogon* + *areolata).*

The polytypic *nigrimontis* is structurally and geographically intermediate between the forms related to *rubromarginata* and *inornata.* Specifically, one may trace gradients in gonopod configurations from *nigrimontis* via *sigirioides* (#50) to *inornata* (#52) and *truncata* (#51), and via *triangulata* (#45), *rubromarginata* (#42), and *austrimontis* (#43) to *whiteheadi* (#44). In the Toe River Valley fauna, *inornata* occurs in the headwaters and therefore at a geographic extreme, and although the geographically intermediate *truncata* is more highly derived in gonopodal features, it shows clearer evidence of past continuity with *inornata* than with *sigirioides.* We have found no satisfactory dichotomous resolution of relationships among members of the *rubromarginata* group.

An instance of geographic discontinuity occurs in the *rubromarginata* group among taxa which should be clinally continuous. *Sigmoria rubromarginata* is restricted to the Blue Ridge Province of North Carolina and Tennessee, and the main population of *austrimontis* is found in the South Mountains, an inselberg chain in the western Piedmont Plateau. Their chief difference involves the distal zones, that of *austrimontis* being twisted mediad to reveal the surfaces of the medial and lateral flanges in medial view, while that of *rubromarginata* faces anteriad to reveal only the edge of the medial flange in this perspective. The range of the South Mountain form is contiguous in the western Piedmont and Blue Ridge escarpment with more variable ones that bridge the anatomical gaps. The latter populations of *austrimontis* have features that suggest intergradation with *rubromarginata,* but the taxa are disjunct by about 30 miles and are considered reproductively isolated. On the Blue Ridge Front in Virginia, *whiteheadi* occurs some 120 miles north-northeast of the nearest population of *austrimontis,* at Morganton, Burke County, North Carolina. Also, *whiteheadi* has yellow stripes instead of red, and the gonopodal resemblance between it and *austrimontis* is not as close as that between the latter and *rubromarginata. Sigmoria (Sigiria) whiteheadi* and *austrimontis* might seem to represent an eastward extrusion into an area between the ranges of *Dixioria* and *Croatania* that should otherwise be occupied by *Sigmoria s. str.,* but the supposed range extrusion violates the underlying hypothesis of simple vicariance partitioning. Rather than *Sigiria* plus *Falloria* as the basal sister element in the genus (Figure 154), that element should be either *Rudiloria* plus *Dixioria,* or *Croatania* plus *Cleptoria.* Resulting vicariance schemes appropriately place *Sigiria* between the ranges of *Dixioria* and *Sigmoria.*

Sigiria includes three yellow/yellow taxa — *areolata, inornata,* and *whiteheadi* — that are neither geographically nor structurally contiguous with one another. This coloration is found among members of several other eastern subgenera and is more probably an "incomplete synapomorphy" than an instance of convergence. Within *Sigiria,* however, this coloration is plesiomorphous. In *whiteheadi,* it is relictual in comparison to the syntopic yellow/black *l. latior (Sigmoria).* In *inornata,* the condition is variable, and, though we lack details, we predict that the populations most proximal to *truncata* are the ones that are red/red. *Sigmoria (Sigiria) inornata* occurs in headwater areas of the Toe River Valley, and its westernmost, downstream populations most resemble *truncata* in gonopodal characters by having longer and flatter peaks, and shorter distal zones. In *areolata,* an obvious sister to *stenogon,* the color is stable so far as known, but the nearest populations of *stenogon* tend to be red/red unlike the purple/purple ones farther south, so that there is a stepped clinal continuum.

Although the *stenogon* group is closely allied geographically and structurally with the *rubromarginata* group, there is no obvious synapomorphy. Therefore, these may not truly be sister groups. Shelley (1981a) allied *nantahalae* (here placed in *Falloria)* with *stenogon,* as the two species then considered to represent the *stenogon* group. We assume that the resemblances were ancestral. This satisfies our premise that *nantahalae* is the sister element within *Falloria,* which despite diversity apparently is truly monophyletic. However, we are not certain that the *stenogon* group is not directly sister to *Falloria* rather than to the rest of *Sigiria.* Thus of the eight subgenera, *Sigiria* is the one least likely to be monophyletic.

Falloria. — This subgenus, (Figures 151-152, areas 56-73) consists of 18 species arrayed among eight species groups. The lineage is defended by geography (proximal only to *Sigiria),* linkages via transformation series, and apomorphous red/blue coloration. No other congeners have this bicolored pattern, which we presume is energetically expensive to acquire and therefore unlikely to be convergent. However, sympatric species of *Brachoria* also display the pattern, which we think represents mimetic convergence rather than "incomplete synapomorphy." In either case the coloration appears to be conserved by mimetic pressure. Two geographically peripheral species, white/white *leucostriata* (#57) and red/white *nantahalae* (#56), have color patterns unique in the genus. Both occur in areas not occupied by red/blue *Falloria* or *Brachoria,* and the absence of mimetic pressure may explain the absence of blue metatergal stripes.

The postulated sister group to *Falloria* is *Sigiria,* particularly the *stenogon* group, which is the basis for out-group comparisons. Northward, where species of *Falloria* are parapatric with those of the *rubromarginata* group, there is abrupt structural discontinuity. Our hypothesis of species group relationships is *Falloria* = *nantahalae* + *(leucostriata* + *(aphelorioides* + *(translineata* + *((tuberosa* + *(bidens* + *picapa))* + *mimetica)))).* This hypothesis is derived from the following considerations.

Aside from derived color pattern, the monobasic *nantahalae* group (#56) lacks gonopodal flanges. The ancestor of its sister group is postulated to have had a sort of hood on the peak of the acropodite.

The *leucostriata* group *(xerophylla,* #58, and *leucostriata,* #57) retains a short process on sternum 4, and its species are disjunct but gonopodally similar. The disjunction is explicable via vicariance partitioning. Its sister group is postulated to have had a medium process of sternum 4 ancestrally.

The monobasic *aphelorioides* group (#59) has a looped acropodite. Its sister group is postulated to have had an enlarged prefemoral process ancestrally.

The ancestor of the *translineata* group had a forked prefemoral process, whereas the ancestor of its sister lineage is postulated to have had the peak of the acropodite dentate ancestrally. The more eastern, Blue Ridge species *(translineata, lyrea, fumimontis,* and *ainsliei,* #60-63) had a more massive acropodite. The more western, Cumberland Plateau ones *(forficata, houstoni,* and *abbreviata,* #67-69) diverged into an easterly form with the process of sternum 4 lengthened and westerly forms in which it was shortened. Therefore, the *translineata* group = *((fumimontis + translineata) + (lyrea + ainsliei)) + (forficata + (houstoni + abbreviata)).*

Relationships among the *bidens, tuberosa, picapa,* and *mimetica* groups are more obscure. In the *bidens* group, the prefemoral process is more or less swollen, with the process of sternum 4 moderate in *bidens* (#64) but shortened in *prolata (*#65). In the Cumberland Plateau of Tennessee, the monobasic *picapa* group (#70) has the process of sternum 4 shortened and shares certain acropodal features with *prolata* of the *bidens* group, so the two groups are sisters. In the Blue Ridge, the *bidens* and *tuberosa* groups are not linked by a satisfactory synapomorphy, but by geographic inference. In the monobasic *tuberosa* group (#66), the prefemoral process is short and the process of sternum 4 is lengthened, in addition to various other distinctive features. In the Nashville Basin, the *mimetica* group has the process of sternum 4 shortened, and it is divergent in having greatly reduced prefemoral processes and massive acropodites in two species. Despite their divergences and disjunctions, the *tuberosa, bidens, picapa,* and *mimetica* groups appear readily interpreted as a once continuous northern vicariad.

The *mimetica* group (*mimetica,* #71, *crassicurvosa,* #73, and *pendulata,* #72) includes a curious population. One sample resembling the two eastern species, *pendulata* and *crassicurvosa,* was found in the eastern part of the range of the westernmost species, *mimetica.* The gonopods of *mimetica* are considerably thinner than those of the other two species (compare figures 111, 117, 123) and are homogeneous throughout the range. However, the above exception has a thicker acropodite with slightly swollen areas suggestive of lobes (Figures 113-114). It may represent a relict of a former connection between *mimetica* and *crassicurvosa,* and it also suggests that the three taxa of the *mimetica* group may be conspecific. The specimens were collected in 1957, and since then the eastern range periphery of *mimetica* and the area between the species has been thoroughly searched without finding more individuals. Consequently, the status of this population is uncertain, and it may be extinct. The massive gonopods of *crassicurvosa* and *pendulata* are synapomorphous. Thus, the *mimetica* group = *mimetica* + (*crassicurvosa* + *pendulata.*)

We propose the following vicariance sequence within *Falloria*. The first vicariance occurred on the southeastern front of the Blue Ridge, separating *nantahalae*. The second separated an eastern *leucostriata* group. The third segregated *aphelorioides* at the southern end of the Blue Ridge, and the fourth caused a south/north separation of the *translineata* group from the *tuberosa, bidens, picapa,* and *mimetica* groups.

This vicariance scheme produces some geographic quirks, notably in disjunctions between the Nashville Basin, Cumberland Plateau, and Blue Ridge. However, it also supplies a plausible explanation for the disjunct ranges of *xerophylla* and *leucostriata*. They are so similar in gonopodal characters that they must once have been continuous, but they now occur at opposite ends of the rugged southern Blue Ridge Mountains and are separated not only by distance and terrain but also by numerous congeners. Here, extinction of intermediates may have been caused by range expansions of other taxa, as suggested by the relatively large ranges of two intervening eastern species, *nantahalae* (*Falloria*) and *rubromarginata* (*Sigiria*).

In *prolata,* isolated in a small pocket of the GSMNP near Gatlinburg, Tennessee, the distal zone curves sublaterad from the peak and is not coplanar with the basal zone. It is similar to that of *picapa* in the Cumberland Plateau and markedly different from the curvatures in *bidens* and the more southerly forms of the *translineata* group, in which the two zones are coplanar. The boundary between *prolata* and *bidens* in the Roaring Fork Nature Trail section of the GSMNP is sharp, as the latter occurs along the more southern entrance road and the former along the more northern exit road. This southern population of *prolata* has a mildly globose prefemoral process characteristic of *bidens* (compare figure 83 with Shelley 1981a, figure 80), unlike the northern, Greenbrier populations (Figures 79-82). The resemblance of the prefemoral process with *bidens* links only the most proximal populations, whereas the acropodal resemblance with *picapa* occurs throughout the range. Thus, the distal zone curvature of *prolata* and the bifurcate prefemoral process of *forficata* form evidence of former links between the Blue Ridge and Cumberland faunas.

Geographic factors indicate that the long sternal processes of *forficata* in the Cumberland Plateau, *tuberosa* in the Great Smoky Mountains of North Carolina, and various piedmont South Carolina species of *Croatania* and *Cleptoria,* represent convergence (see Table 2). *Sigmoria (Falloria) forficata* is separated from *tuberosa* by about 90 miles of the most rugged mountains in the southeast, and some 70 miles and more mountains segregate the latter from the piedmont forms.

In the Blue Ridge, *aphelorioides* has a circular acropodite similar to that of *ainsliei,* but it is placed in a separate species group because the prefemoral process is undivided. Their distributions, moreover, are separated by other species of the *translineata* group. Hence, their looped acropodites probably are convergent, as they also are with *trimaculata (Rudiloria)* and the genus *Apheloria.*

SUBGENERIC RELATIONSHIPS. — Here, we attempt to relate the subgenera of *Sigmoria,* discussed above and mapped in figure 153. We have no satisfactory character state nor transformation series to define the genus *Sigmoria* as monophyletic, but it is defined by its geographic cohesiveness. It has geographic properties similar to those of a single species. When species diverge, there is no theoretical need for both members of a sister pair to be defined by autapomorphies. Here, this applies at the generic level between the sister genera *Sigmoria* and *Deltotaria,* wherein the latter is defined by a satisfactory synapomorphy and represents a now independent overlay in the southern part of the former's range. The sister relationship of these two genera, as discussed under generic relationships later, is postulated on both geographic and structural grounds. We consider slender gonopodal form in the montane *D. brimleii* and in sympatric species of *Falloria* and *Sigiria,* and robust gonopodal form in the piedmont *D. lea* and in species of *Croatania* and *Cleptoria* in that region, evidence of past connections.

Problems with the preliminary subgeneric hypothesis. — The subgeneric arrangement used throughout this paper reflects a clockwise, radial arrangement from *Rudiloria* in the north to *Falloria,* based on the preliminary cladistic hypothesis shown in figure 154. This unsatisfactory, basally trichotomous arrangement specifies an east/west separation between the *Croatania/Cleptoria* and *Falloria/Sigiria* lines, with the geographically intermediate and more southern *Cheiropus* unassigned. The eastern lineage occupied the northern Appalachians and eastern piedmont, and the western lineage occupied the southern Appalachians and Cumberland Plateau. The eastern lineage divided into northern (*Rudiloria/Dixioria*) and southern components, the latter next into eastern (*Sigmoria*) and western (*Croatania/Cleptoria*) lineages.

Superficial gonopodal similarities between sympatric members of *Deltotaria* and *Sigmoria* formed one reason for a basal dichotomy separating *Croatania* and *Cleptoria* to the east from *Falloria* and *Sigiria* in the west. *Cheiropus,* which is geographically intermediate between these presumed sister pairs, does not bear conspicuous relationship to either.

Reasons for linking *Rudiloria, Dixioria,* and *Sigmoria s. str.* to *Croatania* and *Cleptoria* rather than to *Falloria* and *Sigiria* arose principally from the geographic distributions of certain character states and postulated "incomplete synapomorphies" in the lengthened process of sternum 4 and the loss of metatergal stripes. In turn, *Sigmoria s. str.* seemed better tied to *Croatania* and *Cleptoria* than to *Rudiloria* and *Dixioria,* as judged prin-

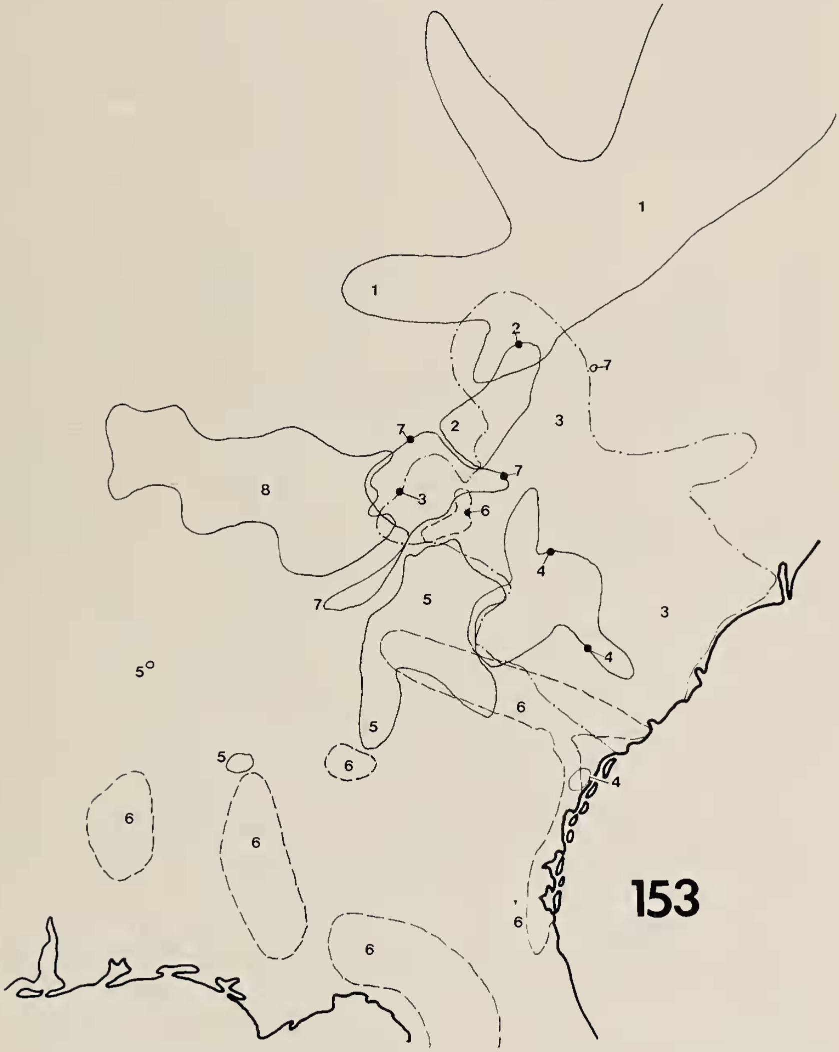

FIG. 153. Distributions of the subgenera of *Sigmoria.* 1, *Rudiloria;* 2, *Dixioria;* 3, *Sigmoria;* 4, *Croatania;* 5, *Cleptoria;* 6, *Cheiropus;* 7, *Sigiria;* 8, *Falloria.*

cipally from some gonopodal similarities in *arcuata (Cleptoria)* and *quadrata (Sigmoria)*.

This scenario is faulty in the following respects:

1. *Falloria* and *Sigiria* are allied, but it is not clear that *Sigiria* is monophyletic. *Falloria* might be directly allied to the *stenogon* group of *Sigiria,* but we found no compelling reason why the *rubromarginata* group might not be linked with *Sigmoria* rather than with *Falloria.* Nonetheless, we provisionally accept *Falloria* and *Sigiria* as true sister groups.

2. We accept *Croatania* and *Cleptoria* as sister groups based on synapomorphies. The argument for linking *Sigmoria* with *Croatania/Cleptoria* contradicts the character argumentation for recognizing basal

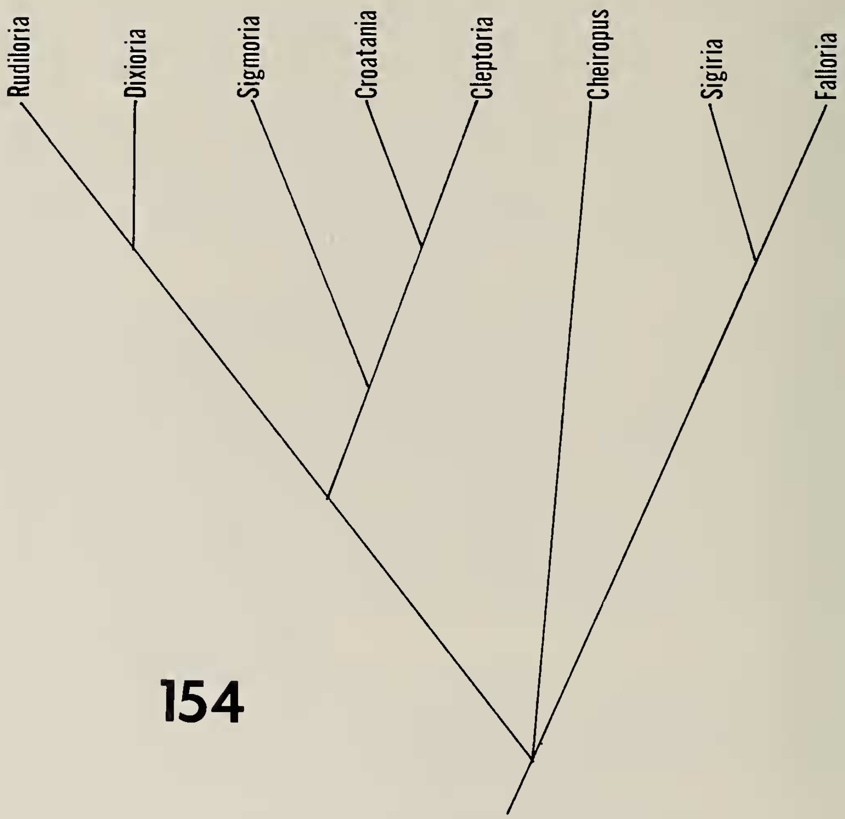

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Fig. 154. Relationships among the subgenera of *Sigmoria*, preliminary hypothesis.

Falloria/Sigiria and *Croatania/Cleptoria* lineages, because it specifies a reversal in gonopodal form from robust to slender, convergent upon that in *Sigiria.*

3. There are evident structural linkages of *Sigmoria* with *Sigiria* and/or *Cheiropus,* and either or both are geographically plausible. The position of *Cheiropus* is enigmatic, yet there are reasons to link it with *Sigmoria.* However, the ensuing hypothesis would have the combined distributions of *Cheiropus* and *Sigmoria* encircling those of *Croatania* and *Cleptoria,* an improbable vicariance scheme.

4. We accept *Rudiloria* and *Dixioria* as sister groups based on synapomorphy. However, proximal taxa of *Dixioria* and *Sigiria* have gonopods sufficiently similar that convergence is implausible. This presents a circular argument, if *Rudiloria* and *Dixioria* are said to have arisen from a lineage which ancestrally had massive gonopods.

5. The northeastward extension of *Sigiria* via *austrimontis* and *whiteheadi,* which separates the ranges of *Rudiloria/Dixioria* from those of *Croatania/Cleptoria,* represents an unnecessary argument for range dispersal made still more implausible by the large gap between *austrimontis* and *whiteheadi.* It can be avoided if *Rudiloria/Dixioria* is considered a basal sister element or otherwise separated from a *Croatania/Cleptoria* lineage. Consider the pizza pie analogy. No matter how irregular the slices, the pie does not actively slice itself. Thus, the postulated range extrusion of the *rubromarginata* group involving *austrimontis* and *whiteheadi* would be unsatisfactory even if there were a clear, extant continuum between the two.

Resolution of the problems. — If we accept *Falloria/Sigiria, Rudiloria/Dixioria,* and *Croatania/Cleptoria* as monophyletic groups, we need to select an appropriate dichotomous vicariance scheme for just five slices. There are 105 possible schemes, but many are geographically untenable as shown by figure 155. For instance, the sister of *Rudiloria/Dixioria* must either be or at least include *Falloria/Sigiria* to account for geographic proximity.

Neither *Cheiropus, Croatania/Cleptoria, Falloria/Sigiria,* nor *Sigmoria* alone represent plausible first cuts, because their distributions are wedge shaped. Hence, the first cut must have been *Rudiloria/Dixioria,* if we assume that one group is sister to the other four. If two groups are sister to the other three, the ones that need consideration are the following. For *Rudiloria/Dixioria,* the only possible pairing is with *Falloria/Sigiria,* and the only plausible triplet arrangement would include *Sigmoria.* For *Croatania/Cleptoria,* linkage could be with *Cheiropus* and/or *Sigmoria.*

An initial separation of *Cheiropus* and *Croatania/Cleptoria* from the rest of the genus based on ancestrally massive versus slender gonopods is geographically plausible, but the groups are divergent from one another and *Cheiropus* shows affinity elsewhere in the genus. In an initial separation of *Rudiloria/Dixioria* and *Falloria/Sigiria* from the rest of the genus, neither

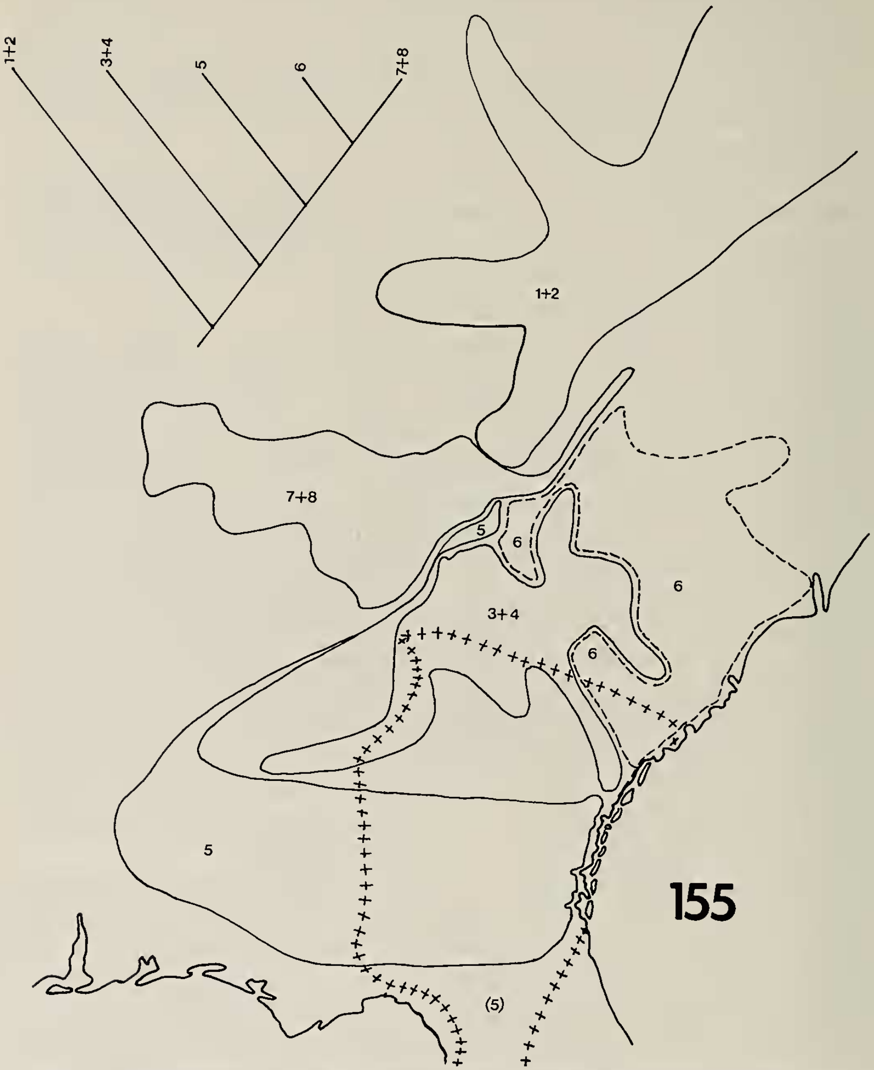

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FIG. 155. Vicariance map and cladogram for the subgenera of *Sigmoria,* numbers as in Fig. 153. The Jefferson Co., AL, record of *rileyi (Cleptoria)* and areas of secondary sympatry of *latior (Sigmoria)* are omitted. 1 + 2, *Rudiloria* + *Dixioria;* 3 + 4, *Croatania* + *Cleptoria;* 5, *Cheiropus* [(5), *planca* group]; 6, *Sigmoria;* 7 + 8, *Sigiria* + *Falloria.*

lineage in the basal dichotomy is supported by a satisfactory autapomorphy. We reject these hypotheses.

We propose *Rudiloria/Dixioria* as sister to the rest of the genus. This is the most probable, geographically simple arrangement and is based on the most satisfactory autapomorphy, although for one lineage only: gonopod orientation in *Rudiloria/Dixioria*. Slender gonopods in *Rudiloria/Dixioria* and proximal *Sigiria* represent the ancestral condition, not convergence, and there are no detailed residual linkages with other groups such as are implied between *Croatania/Cleptoria* and *Sigmoria*. This arrangement also implies convergence rather than "incomplete synapomorphy" in the lengthened process of sternum 4 and color pattern. Thus, the continuum of the *rubromarginata* group of *Sigiria* via *austrimontis* to *whiteheadi* divides the lengthened process of sternum 4 of *Rudiloria/Dixioria* from those of *Croatania/Cleptoria* and southern members of *Sigmoria*. Moreover, the color pattern involving lack of metatergal stripes may represent mimetic convergence, as the distribution of *l. latior (Sigmoria)* completely overlaps that of *Dixioria* rather than being contiguous.

If *Rudiloria/Dixioria* is sister to the rest of the genus, then just four groups and 15 dichotomous arrangements remain. Only *Croatania/Cleptoria* is a geographically and structurally suitable basal element. As in *Rudiloria/Dixioria,* there is an acceptable ancestral autapomorphy for *Croatania/Cleptoria,* the spine or irregular notching on basal zone, but not for the sister lineage.

This leaves just three groups and three arrangements. Our resolution of these is based partly on geography and partly on divergence. *Cheiropus* has elements which are the least similar, perhaps in part reflecting ancestral geographic variations in the genus. Where geographically proximal to *Falloria/Sigiria,* there is little structural resemblance. Geographic connections with *Sigmoria* are in part dissected by the range of *Croatania/Cleptoria,* and where the ranges overlap, as with *l. munda (Sigmoria)* and the *divergens* and *haerens* groups *(Cheiropus),* gonopods are too dissimilar to imply close common ancestry. In contrast, gonopodal similarities of proximal elements of *Sigmoria* and *Falloria/Sigiria* are much stronger.

Relationships among the subgenera. — Our revised cladistic hypothesis (Figure 156) is: genus *Sigmoria = (Rudiloria + Dixioria) + ((Croatania + Cleptoria) + (Cheiropus + (Sigmoria + (Sigiria + Falloria))))*.

This hypothesis represents our best estimate of vicariance partitioning of the subgenera. In the absence of a suitable synapomorphy scheme, which we think does not exist, it is perforce based principally on the geographic distributions of the taxa and their character states considered together. It does not resolve the problems of undefined monophyly of *Sigiria* nor definition of the lineage *Sigiria/Falloria.* However, the only plausible geographic linkage for *Falloria* is with *Sigiria* (or a part of *Sigiria,* the *stenogon* group), and if *Sigiria* is not a natural group the only plausible alternative arrangement is to shift the *stenogon* group to *Falloria.*

Features of the hypothesis are the following:

1. The partitioning pattern (Figure 157) is coherent and sequential, requiring only minimal range alteration and secondary sympatry to achieve the present distributional pattern.

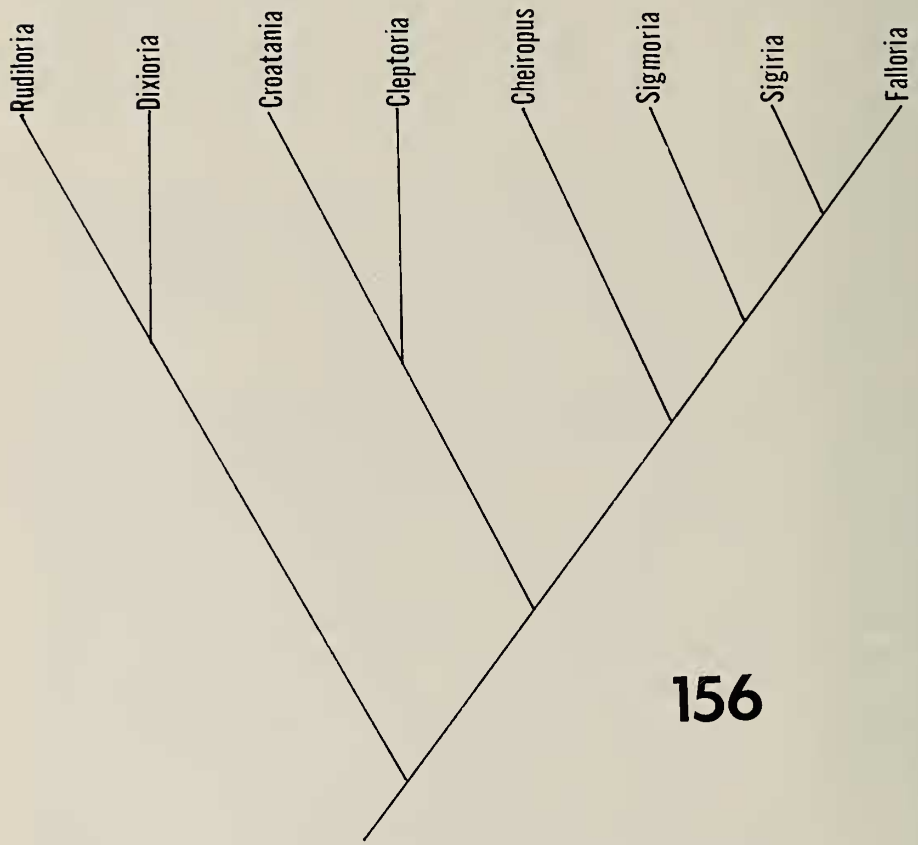

FIG. 156. Relationships among the subgenera of *Sigmoria,* revised hypothesis.

2. The virtual encirclement of *Croatania/Cleptoria* by *Cheiropus* and *Sigmoria s. str.* is geographically illogical and thus probably secondary. Aside from the clearly secondary distribution of the *planca* group, the southern area of *Cheiropus* is represented only by the now disjunct populations of *australis*. That these may be recent immigrants is consistent with their lack of differentiation.

3. The gonopodal similarities between *Rudiloria/Dixioria* and *Sigiria* reflect ancestral similarity, not convergence. Length of the process of sternum 4 is not quite continuous from *Dixioria* to *Sigmoria*.

The ancestral similarity features implied by items 4-6, both somatic and gonopodal, are ones that cross indicated cladistic lines. We conclude that they are plesiomorphous, not apomorphous.

DISCUSSION. — Traditional cladistic analysis assumes that lineages are independent and definable by autapomorphies, and where apparent conflicts occur they are resolved by parsimony techniques. The traditional analysis is based solely on character information, *independent from* geography. Our first assumption must always be that a character based cladistic hypotheses is attainable, regardless of initial impressions. Even after realizing that *Sigmoria* was a geographic mosaic, we still attempted traditional analysis. It failed. Our initial attempts involved the taxa first reviewed by Shelley (1981a) and were based on color, body size, details of gonopodal structure, and even ecology. We found virtually complete noncongruence between all characters studied and could only conclude that *Sigmoria* as it then stood could not be monophyletic, despite patterns of geographic contiguity among character states. Parts of the puzzle seemed to be missing.

The conclusions about relationships reached in this paper need to be tested by rigorous cladistic analysis, but we contend that such analysis will require substantially more critical information such as might derive from facial chaetotaxy and comparative body chemistry. Nearly all of the characters and character conditions that we presently have for analysis are homoplasious.

Therefore, the key to solving relationships within *Sigmoria* is the realization that the genus is a geographic mosaic. Its autapomorphy is geographic cohesiveness; *Sigmoria* has the geographic properties of a species. Its minimal divisions, the species and subspecies, also are geographic entities, with allopatric and/or parapatric relations to other such divisions. Character states map in cohesive geographic patterns but are noncongruent with one another. The *only* way to analyze the mosaic based on presently available character data is to *include* geography.

In our analysis of major components, we combined geographic and cladistic inference to refute the null hypothesis that the genus *Sigmoria* was a continuum. We tested the subgenera as stationary vicariads in our analysis of relationships. In both cases, spatial configurations are the critical factor.

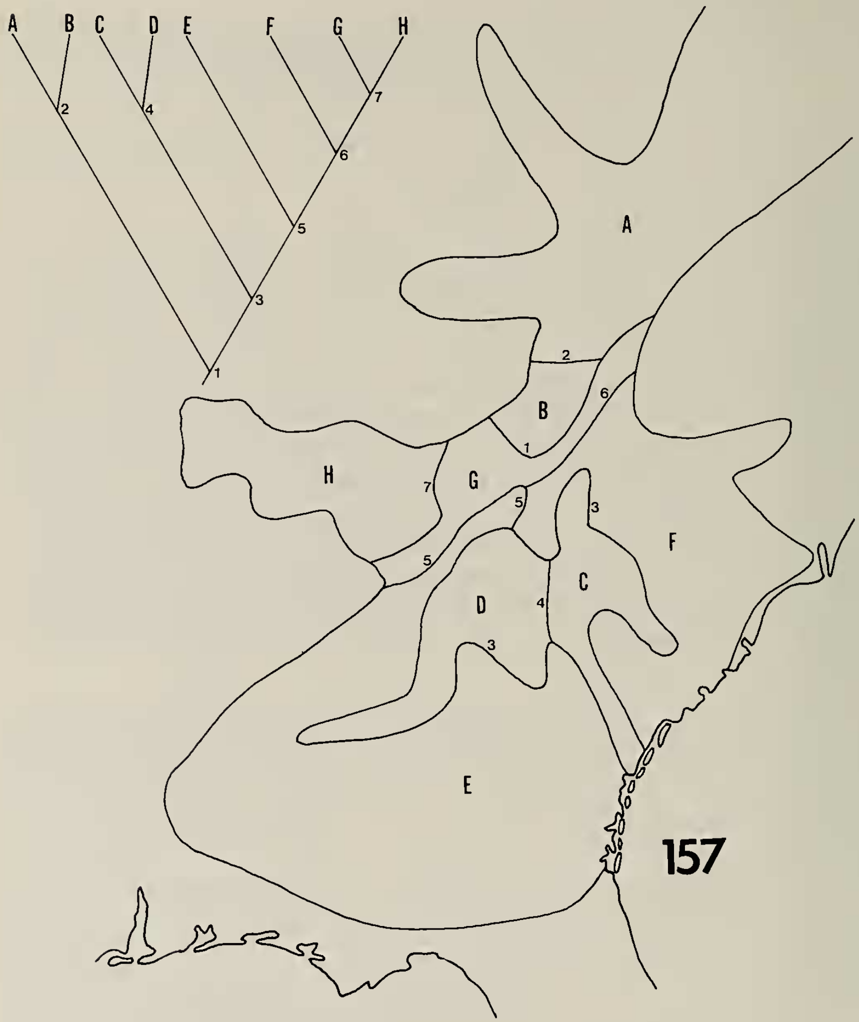

Fig. 157. Partitioning system and cladogram for the subgenera of *Sigmoria*. A, *Rudiloria;* B, *Dixioria;* C, *Croatania;* D, *Cleptoria;* E. *Cheiropus;* F, *Sigmoria;* G, *Sigiria;* H, *Falloria*.

In traditional cladistic analyses, both lineages of a sister pair are defined by autapomophies. However, in *Sigmoria,* rarely are both members of geographic pairs thus defined. This situation merely reflects the evolutionary history of the mosaic, which was created by simple vicariance partitioning. Both divergence and extinction are largely absent from the system. Though we were forced to use geographic distributions alone to determine sequencing, we are satisfied with the accuracy of the method although it lacks the persuasive force of traditional character analyses. The method should pertain to all tightly fitted allopatric/parapatric mosaics. For their resolution, major component analysis using both geographic and character distribution inference is the only recourse available. In *Sigmoria* it is easier to analyze cladistic (character) relationships within the subgenera than between them. These units are segments of the geographic whole, and thus their constituent parts are less divergent and demonstrate more obvious linkage patterns.

It is ironic that a thorough analysis of *Sigmoria* lends credence to the judgement by Hoffman (1958a) that it had become a "catch-all" genus. Now, it is much more so, because it has "caught" all relevant pieces of a biological mosaic. All of the subgenera, previously considered genera, represent only fragments of a single geographic entity. *Sigmoria* thus is larger than anyone previously imagined. What we now call *Sigmoria* is an enormous apheloriine mosaic complex that blankets eastern North America. We might speculate on its origin, how it came to cover so large an area, and the nature of the vicariance mechanisms, but the important fact is that vicariance did take place. Various ancestral character clines were irregularly fragmented to create the present picture. Extinctions and dispersals seem to have played a negligible role. What seems to be active, dispersalist speciation is only the passive result of vicariance. The animals do not actively explore new areas and environments. Instead, they remain in one place and eventually become isolated. The resultant localized populations are reflected in the phenotypes that we interpret as reproductive isolates.

The story of *Sigmoria* still may be incomplete. Other chapters may unfold when *Apheloria* and *Brachoria* are reexamined. Future workers may conclude that *Sigmoria* must be submerged under one of these older names, particularly *Brachoria,* although we think they form separate mosaics. The forms assigned to *Brachoria* have "sigmoid" acropodites that fall within the range of curvatures in *Sigmoria.* Published drawings show apparent medial flanges, teeth on the medial and undersurfaces of the peaks and distal zones, and various other acropodal modifications comparable to conditions found in *Sigmoria.* The cingulum on the outer surface of the acropodite, which we regard as autapomorphous for *Brachoria,* might really be of polyphyletic origin as it occurs at different relative positions. However, a test for homology may be possible by doing the same kind of major component analysis as we have done for *Sigmoria.*

We think *Sigmoria* can serve as an example in diplopodology of a geographic mosaic, a highly partitioned but still cohesive entity in which differentiation must be rapid. Problem groups, in which accurate delineation of species or genera is difficult, exist throughout the class. In the Polydesmida the xystodesmid genera *Rhysodemus* and *Nannaria* may have as many as 100 and 200 species respectively (Hoffman 1964, 1966, 1970), and the chelodesmid genus *Chondrodesmus* has over 40 weakly differentiated ones (Hoffman 1978b). In the Spirobolida, the Rhinocricidae is renowned for its internal confusion. Hoffman (1969, 1978b, 1979) suggested that these groups are in expanding phases of evolution and actively speciating. We agree that speciation is taking place, but we think it is accomplished passively through vicariance. These and such polydesmoid taxa as *Amplinus* and *Pycnotropis* (Platyrhacidae) and the phenotypically similar California xystodesmids *Xystocheir, Paimokia, Motyxia,* and *Amplocheir* (Xystocheirini) probably are other examples of large, complex mosaics with clines and gradients that have been randomly split by vicariance events, some of which are incomplete. In poorly vagile millipeds, dispersal probably plays only a minor role in the speciation process.

The insight on mosaics derived from *Sigmoria* should apply also to other animal groups with allopatric/parapatric patterns. For example, one may think of systems of isolated mountain peaks, caves, or sand dunes and their specialized beetle faunas. As with the Diplopoda, these mosaic patterns reflect inherent nonvagility. In more highly vagile animals, mosaic patterns may be dictated by extrinsic biotic factors, such as critical host plant associations or mimetic complexes. In such situations, the mosaic must be identified and its pieces analyzed, requiring detailed distributional information as has been compiled for *Sigmoria.* We have identified the shapes of its constituent basic pieces, the species and subspecies; analyzed the relative fits of these pieces to one another; and provided an internally consistent, working hypothesis of relationships for future workers to test. It remains for them to complete the analysis of the Apheloriini by applying these procedures to *Apheloria* and *Brachoria* and then to reexamine *Sigmoria* to determine if it should be submerged under one of these older names. To facilitate this process, we conclude with a review of the apheloriine genera, an analysis of their relationships as far as possible, and an analysis of the affinities among the four principle eastern xystodesmid tribes.

PART VII: THE GENERA OF THE TRIBE APHELORIINI

By Rowland M. Shelley

Tribe APHELORIINI Hoffman

Apheloriini Hoffman, 1979:158, 187.

Components: Apheloria Chamberlin, 1921; *Brachoria* Chamberlin, 1939; *Dynoria* Chamberlin, 1939; *Sigmoria* Chamberlin, 1939; *Deltotaria* Causey, 1942; *Furcillaria* Shelley, 1981.

Diagnosis. — Relatively flexible Xystodesminae of moderate to large size; midbody sterna broad and flat or with variable grooves or impressions, without elevations, caudal edges straight or only slightly produced, without lobes or spines; anterior tarsal claws of males normal, bisinuate; gonopods small to large; sterna connected by membrane only, without sternal remnant; coxae with or without variable apophyses arising on anterior sides, extending ventrad; prefemoral process present or absent, when present variably curved and elongate, often enlarged or subglobose basally, never acicular; telopodite usually entire, occasionally divided or with separate solenomerite, usually curving anteriad, anteriomediad, or mediad in sigmoidal, semicircular, or circular configurations, occasionally linear, usually twisted or with torsion at 1/4 to 1/3 of total length, resulting in crossing of prostatic groove from medial to lateral surfaces; cyphopods with variable receptacle.

Distribution (Fig. 158). — Eastern North America from northern New England to south-central Wisconsin (passing through southern Ontario and the lower peninsula of Michigan) south to Baton Rouge, Louisiana, southern Alabama and Mississippi, and just north of Tampa, Florida. Longitudinally, the tribe is known from the Atlantic seaboard from northern Florida to Virginia, New Jersey to Connecticut, and near the coast in Maine to southeastern Nebraska and eastern Oklahoma. The shaded area in figure 158 was determined from published records in Chamberlin and Hoffman (1958) and Keeton (1959, 1965) plus specimens I have personally collected or seen in museum and private collections. The contrast between the smooth northern and irregular southern boundaries is striking, but the northern distribution has not been as thoroughly studied and its evenness may reflect insufficient sampling. I also slightly extended the northwestern corner into southeastern South Dakota, since the presence of *Apheloria* at Omaha, Nebraska (see *Apheloria* account), suggests potential occurrence in riparian habitats farther north along the Missouri River.

Remarks. — This revised diagnosis incorporates no real changes from the original by Hoffman (1979), but it is substantially expanded to better contrast the Apheloriini with the other major eastern tribes — Rhysodesmini, Nannariini, and Pachydesmini (see Hoffman 1960, 1964; Shelley 1984c). The date of proposal of *Deltotaria* is also corrected to 1942.

Just as colors and color patterns tend to cluster within *Sigmoria s. lat.*, they also do within the *Apheloriini* as a whole and between tribes, and this probably represents mimetic convergence. For example, populations of *I. latior* and *stenoloba (Sigmoria)* with uniformly black metaterga occur sympatrically in Wilkes and Ashe counties, North Carolina, with forms of *Pleuroloma flavipes* having the same markings, and as mentioned earlier the various striped patterns in *Sigmoria s. lat.* tend to overlap areas where

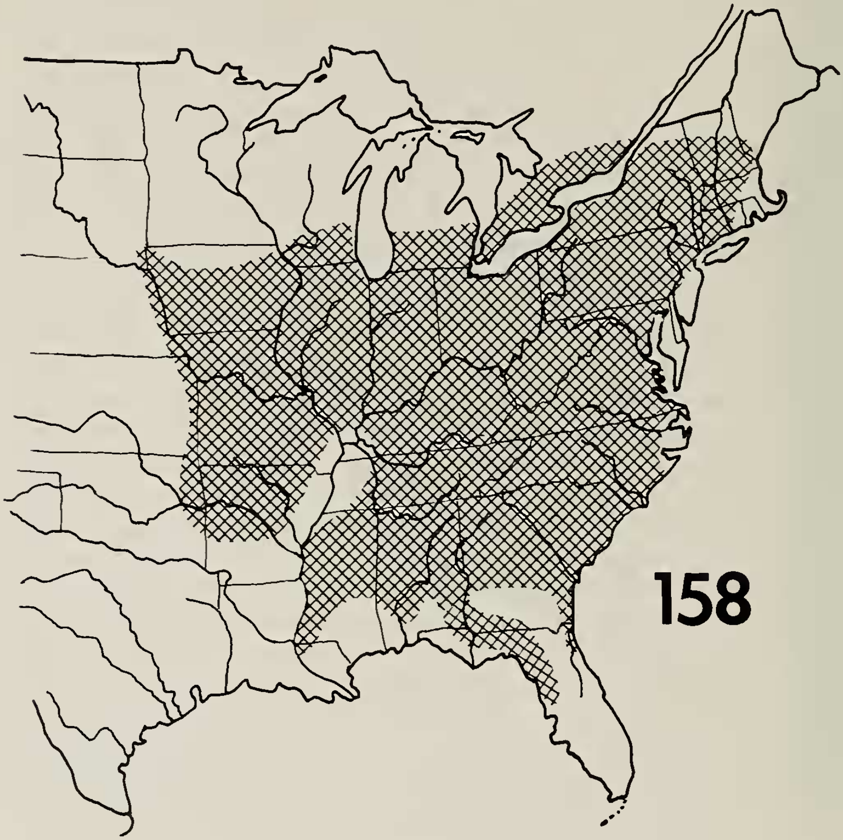

Fig. 158. Distribution of the Apheloriini.

they are also exhibited by *Dynoria, Furcillaria,* and *Brachoria.* I was repeatedly frustrated in searches for the subgenus *Falloria* in the Cumberland Plateau of Tennessee by the recovery of large numbers of red/blue forms of *Brachoria* and none or only a few of *Falloria.* For example, in a large series of red/blue forms from Rainbow Lake, Hamilton County, there were seven males of *B. hubrichti* Keeton and only one of *S. (F.) forficata.* This color pattern in *Brachoria* extends into Alabama approximately to Birmingham, but knowledge of its complete range must await revision of this genus and more field work in Kentucky. However, the extent of the red/red pattern can be reported and is shown in Figure 159. There are two large areas separated by a narrow gap in Piedmont, Georgia. One extends from eastern Tennessee through the Carolinas to piedmont and coastal Georgia, with a branch swinging northward into southeastern North Carolina, and the other begins in central and western Georgia, curves into southern Alabama, widens in a northerly direction to the northwestern corner and adjacent Mississippi, then angles to the Mississippi River. The actual northern and western limits in Alabama and Mississippi are uncertain because of inadequate knowledge of *Brachoria,* but from my limited personal experience these colors are displayed by forms in northern and central Alabama and northern and southwestern Mississippi. The area is extended to Baton Rouge, Louisiana, as *Brachoria* is now known to occur there (see *Brachoria* account) and these were the colors of a female I collected in 1980 in Claiborne County, Mississippi, along the Mississippi River between Vicksburg and Natchez, about 100 miles north of Baton Rouge.

Genus APHELORIA Chamberlin

Apheloria Chamberlin, 1921:232
Leptocircus Attems, 1931:67, preoccupied by *Leptocircus* Swainson, 1833; (Jeekel 1971).

Type species. — Of *Apheloria, Fontaria montana* Bollman, 1887, by original designation; of *Leptocircus, L. inexpectatus* Attems, 1931, by original designation.

Diagnosis (adapted from Hoffman 1978a). — Telopodite set subterminally on coxa, latter projecting distad *in situ* beyond base of prefemoral region; acropodite with torsion, in configuration of tight coil of around 340°, bent abruptly dorsad apically.

Ecology. — The species of *Apheloria* appear to have less specific habitat requirements than most of those of *Sigmoria s. lat.* and are somewhat similar to *latior (Sigmoria)* in being ecological generalists. They occur under logs, rocks, and leaves in mixed deciduous forests as well as in many cove and stream environments. Thus in the Blue Ridge, Ridge and Valley, and Cumberland Plateau Provinces, one is more likely to encounter *Apheloria* on wooded hillsides than any other apheloriine genus, and it is often syntopic with the rhysodesmine genus *Cherokia*. With the exception of *latior*, *Apheloria* is encountered in disturbed and urban habitats to a much greater degree than any other member of the tribe.

Distribution. — The northern 2/3 of eastern North America from a line extending from central New York through southern Ontario, southern Wisconsin, and northern Iowa south to central Arkansas, northern Alabama, and northern South Carolina; longitudinally from along the Atlantic Ocean from southeastern North Carolina to central Connecticut west to eastern Oklahoma and southeastern Nebraska. A recent collection has established its presence on Bald Head Island off the coast of North Carolina.

Species. — Exact total unknown. Hoffman (1978a) listed 14 names that were based on specimens having gonopods identical or similar to those of *montana* and indicated that most were synonyms or at best had subspecific rank. However, another name has since been added to the list, as I reported (1980b) that *Julus virginiensis* Drury, 1770, was based on a form of

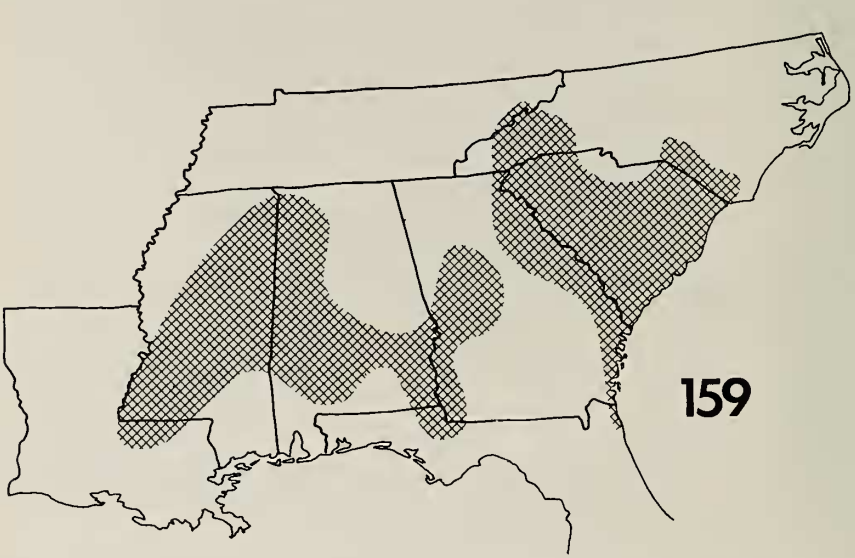

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Fig. 159. Approximate distribution of the red paranota/red metatergal stripe color pattern in the Apheloriini.

Apheloria. It is obviously much older than the other names and thus has taxonomic priority.

Remarks. — Since it is the oldest name in the tribe, taxonomic decisions in the Apheloriini may need modification when *Apheloria* is revised. However, I think it and *Brachoria* comprise separate mosaic complexes which overlie each other and *Sigmoria s. lat.* to varying degrees and thus are generically distinct. The species of *Apheloria* also have different ecological properties, a fact that seems taxonomically significant. Another factor that may warrant consideration is the size, shape, and variation of the process of the 4th sternum in males. As shown in Table 2, it varies greatly in *Sigmoria s. lat.* and knowledge of its condition in *Apheloria* and *Brachoria* may clarify affinities among the genera.

As a final note, I suggest that *Fontaria luminosa* Kenyon (1893) is referable to *Apheloria.* Chamberlin and Hoffman (1958) listed the binomial under "uncertain generic position", and its identity has been an enigma. The type specimen(s) are lost, and the type locality is Omaha, Douglas County, Nebraska. According to Kenyon, the male genitalia curve "inward, forward, outward, and downward," a characterization applicable to *Apheloria* and how a non-specialist might describe the circular acropodite when viewed *in situ.* In August 1983 I found a xystodesmid sample from Omaha in the NMNH consisting of one male and three females labeled, "*Fontaria luminosa* (Type?)." Unfortunately, the gonopods of the male were missing, but from knowledge of xystodesmid distributions, only three species are potential inhabitants of eastern Nebraska — *Pleuroloma flavipes* Rafinesque (Shelley 1980b), *Semionellus placidus* (Wood) (Chamberlin and Hoffman 1958), and a form of *Apheloria* (Chamberlin and Hoffman 1958, plus knowledge I have derived from museum holdings). The specimens are not *P. flavipes* because they lack the diagnostic sternal lobes (Shelley 1980b), and they are much too large to be *Semionellus placidus.* By elimination they must be a form of *Apheloria* if the locality is correct, and the question mark concerned the designation as type, not the place of collection. I think Omaha must be considered accurate, and assignment to *Apheloria* is compatible with Kenyon's description. The matter can be finalized by collection of an adult male in the general vicinity of Omaha or Lincoln, where Kenyon (1893) reported a sight record. With the occurrence of *Apheloria* in eastern Nebraska now fairly certain, its discovery can be reasonably predicted in riparian habitats along the Missouri River in southeastern South Dakota. The name, *luminosa,* also has priority for midwestern forms of *Apheloria,* being 38 years older than Attems' name, *inexpectatus.*

Genus BRACHORIA Chamberlin

Brachoria Chamberlin, 1939:3.
Tucoria Chamberlin, 1943b:17.
Anfractogon Hoffman, 1948:94.

Type species. — Of *Brachoria, B. initialis* Chamberlin, 1939, by original designation; of *Tucoria, Fontaria kentuckiana* Causey, 1942, by original designation; of *Anfractogon, A. tenebrans* Hoffman, 1948, by original designation.

Diagnosis. — Acropodite with torsion, bisected at various positions by distinct cingulum.

Ecology. — I have collected forms referrable to *Brachoria* in a variety of habitats. In western North Carolina they can be found in mixed deciduous forest and cove environments. In the Cumberland Plateau of Tennessee and Alabama they occur in the latter or along streams in the most moist spots available. Farther south in Alabama and in Mississippi, they occur only in deciduous environments along streams.

Distribution. — As shown by Keeton (1959) and Hoffman (1971), *Brachoria* extends in a northeast-southeast direction from a center of abundance in the Cumberland Plateau Province. It is known as far north as Fayette County, Pennsylvania (Carnegie Museum of Natural History), and southeastern Indiana; as far east as the Blue Ridge Front in McDowell County, North Carolina (Shelley 1979b); and as far south as Lee County, Alabama, and East Baton Rouge Parish, Louisiana (FSCA).

Species. — Twenty nine are now recognized, one with three subspecies.

Remarks. — I indicated (1979b) that a second revision of *Brachoria* was needed to consider the nomenclature changes since Keeton's revision (1959) and include newly collected material. Such a study is as important as a revision of *Apheloria,* and *Brachoria* could be assigned top priority because it has more species. Although defined by the acropodal cingulum, presumably an autapomorphy, I am not certain *Brachoria* is monophyletic because the location of the cingulum varies, suggesting independent evolution from two or more ancestral stocks. Thus, a synonym may have to be revived or a new genus proposed to accommodate some forms. These are matters that should be addressed in a second revision.

Genus DYNORIA Chamberlin

Dynoria Chamberlin, 1939:7.

Type species. — *D. icana,* Chamberlin, 1939, by original designation.

Diagnosis. — Acropodite without torsion, prostatic groove running entirely along medial surface; divided at 2/3-3/4 length into lateral tibial process and medial solenomerite branch.

Ecology. — My only field encounter with *D. icana* was in Oconee County, South Carolina, where I found it under a thick layer of leaves in a slight depression in an oak-hickory forest near Hartwell Reservoir (Shelley 1984b). It also occurs on the edge of the Blue Ridge Province, but there are no ecological notes on collecting labels. In Georgia, *D. medialis* is found in typical piedmont habitat, under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — Southeastern extremity of the Blue Ridge Province in North Carolina and Georgia, extending onto the Piedmont Plateau of western South Carolina, and the Piedmont and Coastal Plain of central and southwestern Georgia (Shelley 1984b).

Species. — Two, one in each of the above described regions.

Remarks. — *Dynoria* is the only apheloriine genus lacking torsion, and along with *Furcillaria,* one of only two with a distally divided acropodite. I indicated (1984b) that they comprise a separate evolutionary branch in the Apheloriini, but as shown in Figure 160, they actually represent distinct lineages because torsion constitutes a synapomorphy between *Furcillaria* and the other tribal components. I also proposed a dispersal mechanism for evolution of *Dynoria* and *Furcillaria,* but this scheme is inoperative. The animals are not sufficiently vagile for dispersal to be more than a minor factor in their evolution; instead, vicariance is operative.

Genus FURCILLARIA Shelley

Furcillaria Shelley, 1981c:953-955.

Type species. — *F. aequalis* Shelley, 1981, by original designation.

Diagnosis. — Acropodite with torsion, prostatic groove crossing to lateral surface near 1/3 length; divided at 2/3-3/4 length into lateral tibial process and medial solenomerite branch.

Ecology. — The species of *Furcillaria* occur under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — A triangular area in the Piedmont Plateau of South Carolina between the Pacolet and Savannah Rivers, extending to the western tip of the state in Oconee County. The species are allopatric and occupy narrow bands within the generic range.

Species. — Three.

Part VIII. Relationships in the Tribe Apheloriini

By Rowland M. Shelley and Donald R. Whitehead

Shelley (1981a) deferred discussion of generic affinities of *Sigmoria* until taxonomic knowledge of the other apheloriine genera could be brought to comparable levels. This has since been done for all except *Apheloria* and *Brachoria,* so we now provide preliminary assessments of relationships among the genera and eastern xystodesmid tribes. Important recent works on the Rhysodesmini and Pachydesmini are those by Shelley on *Pleuroloma* (1980b) and *Dicellarius* (1984c). None has appeared on the Nannariini, but Hoffman (1964) presented a modern tribal diagnosis.

Out-groups used to infer plesiomorphic and apomorphic character states in the Apheloriini are the three other eastern xystodesmid tribes: Rhysodesmini, Pachydesmini, and Nannariini. For tribal comparisons, Rhysodesmini serves as the out-group; although well represented in the east, it also occurs from southern Texas and New Mexico to El Salvador, where it is the sole xystodesmid tribe. The only eastern species not included in these comparisons is *Semionellus placidus,* which is not a member of the endemic eastern tribal complex of Nannariini, Pachydesmini, and Apheloriini. A member of the Chonaphini and related to species in the Pacific Northwest (Hoffman 1979), it has a much more slender form than do other eastern xystodesmids, and its gonopods are divergent in having the acropodite simple and the prefemoral process strongly modified.

The Generic Hypothesis. — The following character statements document the generic hypothesis in figure 160: Apheloriini = *Dynoria* + *(Furcillaria* + *(Apheloria* + *Brachoria* + *(Deltotaria* + *Sigmoria))).*

1. *Presence or absence of gonopodal torsion.* In all apheloriine genera *except Dynoria,* the acropodite is twisted at 1/3 to 1/2 length, causing the prostatic groove to cross from the medial to the lateral surfaces. This is true even for the *planca* group of *Sigmoria,* wherein the structure is basically curvilinear. Conversely, all pachydesmines except *Dicellarius okefenokensis* and all rhysodesmines and nannariines lack torsion, and the entire course of the prostatic groove or nearly so is visible in medial view. Presence of torsion is therefore considered autapomorphous.

2. *Acropodite divided or undivided.* The acropodite is divided in *Dynoria, Furcillaria,* the Pachydesmini, and many taxa of the Rhysodesmini and Nannariini. An undivided acropodite is autapomorphous in other Apheloriini. An autapomorphous, lateral solenomerite in the *haerens* and *planca* groups of *Sigmoria* is not homologous with the apically divided acropodite.

From this point on, we have found no clear synapomorphies to specify sister group relationships. The following are generic features.

3. *Acropodal ground plan circular or "sigmoid."* The acropodite in *Apheloria* forms a tight, nearly circular coil. The acropodites of *Furcillaria, Brachoria, Deltotaria,* and most species of *Sigmoria* are basically "sigmoid." The nearly circular loops of *Sigmoria ainsliei, aphelorioides,* and *trimaculata* differ from those of *Apheloria* and are considered convergent. The only other known xystodesmid with coiled acropodites is the oriental genus *Parafontaria,* placed because of other characters in a separate subfamily by Hoffman (1979). The coiled acropodite of *Apheloria* is apomorphous if the genus belongs to a group excluding *Furcillaria* as specified by character 2 and if the "sigmoid" acropodite of *Furcillaria* is homologous to that of *Brachoria, Deltotaria,* and *Sigmoria. Apheloria* may be sister to *Brachoria + (Deltotaria + Sigmoria),* but we found no synapomorphy for them.

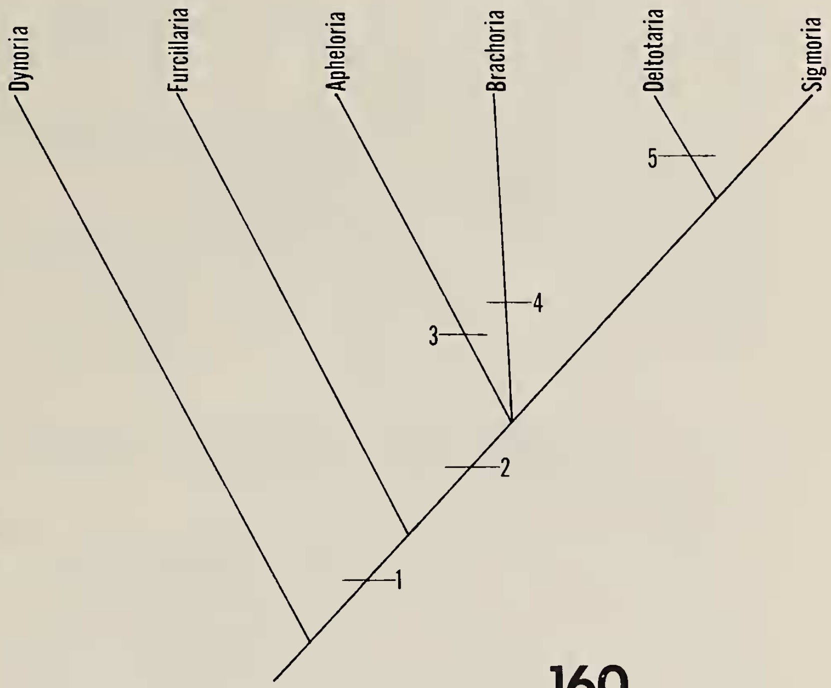

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FIG. 160. Generic relationships in the Apheloriini. The numbers refer to apomorphies discussed in the text.

4. *Presence or absence of a gonopodal cingulum.* A cingulum, or transverse depression on the outer surface of the acropodite stem, is unique to *Brachoria* and is considered autapomorphous pending review of this genus. The acropodite is set off from the prefemur by a cingulum in the rhysodesmine genus *Cherokia* (Hoffman 1960), but we know of no other xystodesmid genus with one on the acropodite blade in each component species.

5. *Presence or absence of a coxal apophysis.* An apophysis, or ventrally directed projection on the gonopodal coxa, is independently apomorphous in *Deltotaria, Pachydesmus,* and *Xystodesmus* (Hoffman 1956b, 1958b; Shelley 1984c).

Deltotaria is considered sister to *Sigmoria,* partly from overall geography and partly from geographic congruence in general gonopodal form between members of each genus. We are aware of no autapomorphy for *Sigmoria* or for *Sigmoria* + *Deltotaria. Apheloria, Brachoria, Deltotaria,* and *Sigmoria* are partly sympatric, overlying mosaics. If each is viewed as having geographic properties of a species and thus originally allopatric, *Apheloria* may be considered northern, *Brachoria* western, *Deltotaria* southern, and *Sigmoria* eastern. Aside from congruence in gonopodal features, *Deltotaria* fits best with *Sigmoria* geographically.

The Tribal Hypothesis. — The following character statements document the tribal hypothesis in figure 161, eastern Xystodesmidae = Rhysodesmini + (Nannariini + (Pachydesmini + Apheloriini)).

6. *Retention or loss of a sternal remnant between the gonopodal coxae.* Gonopods are specialized ambulatory appendages, primitively joined by a sclerotized sternum. Retention of a sternal remnant is one of the characteristics of the Rhysodesmini (Hoffman 1960). Sclerotization is replaced by membrane in the other three tribes, an autapomorphous condition.

7. *Condition of pregonopodal tarsal claws in males.* The Nannariini is characterized by apomorphous twisted, spatulate, pregonopodal tarsal claws in males. In other genera the claws are bisinuately curved or uncinate, the plesiomorphic condition.

8. *Presence or absence of lateral subcoxal spines on postgonopodal sterna of males and midbody sterna of females.* These spines or lobes are found in the Nannariini and most rhysodesmine genera. In the Pachydesmini and Apheloriini, the caudal sternal edge is straight except for segments 8-10 where bicruciform grooves create a lobed appearance in some species. Absence of subcoxal spines or lobes is tentatively considered to be apomorphous.

9. *Body size.* The Nannariini and many of the eastern Rhysodesmini tend to be relatively small, whereas most species of Pachydesmini and Apheloriini are large *(Dicellarius okefenokensis, Sigmoria sigirioides,* and

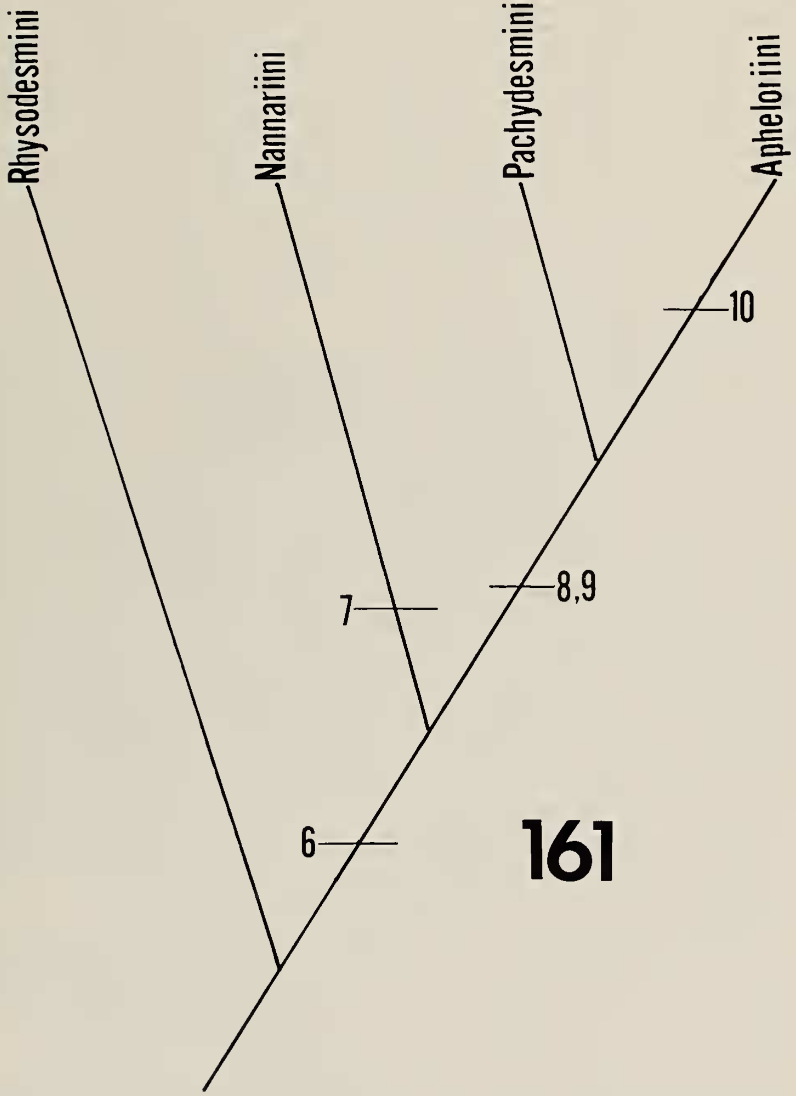

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FIG. 161. Relationships among the four major xystodesmid tribes in eastern North America. The numbers refer to apomorphies discussed in the text.

S. truncata being exceptionally small). Large body size thus appears to be apomorphous and in combination with characters 7 and 8 joins the tribes Pachydesmini and Apheloriini as a monophyletic group.

10. *Condition of the prefemoral process.* Except for occasional individuals of the pachydesmine species *Dicellarius okefenokensis,* the prefemoral process is long, slender, and acicular in the Rhysodesmini, Nannariini, and Pachydesmini and therefore is considered plesiomorphous. In the Apheloriini, it is present or absent, but never acicular.

If monophyly in the Apheloriini is based on nonacicular prefemoral processes, we lack an autapomorphy for the Pachydesmini. Other known structural distinctions between the Pachydesmini and Apheloriini all involve exceptions, and tribal distinction may be unwarranted. Placement of *Dicellarius* and *Thrinaxoria* in the Pachydesmini by Shelley (1984c) was based on the similarity in character 10. The acropodite is divided in the Pachydesmini and undivided in the Apheloriini except in *Dynoria* and *Furcillaria.* All pachydesmines except *D. okefenokensis* lack acropodal torsion, and all apheloriines except *Dynoria* have it. Likewise, the acropodite is linear in all pachydesmines except *D. okefenokensis,* and curved or ''sigmoid'' in all apheloriines except *Dynoria* (secondarily curvilinear in the *planca* group of *Sigmoria).* Among genera of the Pachydesmini, *Pachydesmus* has coxal apophyses (convergent with those of *Deltotaria* in the Apheloriini) and large postgonopodal sternal elevations or podosterna (Hoffman 1958b), both conditions being autapomorphous. *Dicellarius* and *Thrinaxoria* have reduced cyphopodal receptacles, also autapomorphous. We have found no autapomorphous feature for all three genera, and this plus the exceptions regarding divided acropodites and torsion suggest that the two tribes should be combined. However, colors and color patterns may be as useful for characterizing tribes as they are for species within *Sigmoria,* but we have insufficient out-group information to assess polarity. The basic color pattern in the Apheloriini is a black body with bold paranotal spots and metatergal stripes. In contrast, the color pattern is generally pale among the Pachydesmini. Perhaps this lack of pigmentation in the Pachydesmini represents the missing autapomorphy.

Discussion. — These are not character rich hypotheses for either tribal or generic relationships. Other traits, such as facial chaetotaxy and meristic characters of the head and body, have not been analyzed sufficiently for interpolation.

Our comments on *Sigmoria* as a cohesive generic mosaic with a geographic structure virtually that of a single species led to speculation that the genus might be recent. It follows that much of the eastern xystodesmid fauna also may be recent. The endemic tribes Nannariini, Pachydesmini, and Apheloriini, respectively with 2, 3, and 6 genera, form a monophyletic group. The putative sister group, Rhysodesmini, is presumed monophyletic, but we think it probably is not. Points of interest are these:

1. There is very little somatic differentiation among the endemic tribes. Distinctions between them and their genera and species are primarily gonopodal. Occasionally, species with very different gonopods are linked by intermediates (as in the *Sigmoria mimetica* group, for instance), so that gonopodal differences may be less significant than thought. Lack of somatic differentiation is consistent with suggested lack of age.

2. Failure to generate satisfactory cladistic hypotheses at the generic and tribal levels implies lack of extinctions needed to create structural gaps for definitions of lineages. Lineages are ill defined because of retention of ancestral features. Lack of profound structural gaps also is consistent with suggested lack of age.

3. We have reservations about the tribal classification proposed by Hoffman (1979), but the information at hand is insufficient to effect changes. Certainly, the distinction between the Pachydesmini and the Apheloriini does not appear to withstand scrutiny, and we do not think the picture among the entire eastern xystodesmid fauna is yet clear enough to determine where tribal limits should be set. Again, the absence of intensive analyses of *Apheloria* and *Brachoria* is a major gap in our knowledge, but comprehensive study is also needed in the Rhysodesmini. This tribe is both somatically and gonopodally diverse, and may need division. Neither Hoffman (1978c) nor Shelley (1980b) could adequately relate *Caralinda* to other rhysodesmines, and two recently discovered, small-bodied southeastern genera, *Parvulodesmus* and *Gonoessa* (Shelley 1983b, 1984d), are unique in having extremely long acropodites that overlap two or more segments *in situ.* We cite large body size as apomorphous for Apheloriini plus Pachydesmini, but small body size applies to the Nannariini and an increasing number of Rhysodesmini even though the largest xystodesmid of all, *Rhysodesmus dasypus* (Gervais), in Veracruz, Mexico, belongs to this tribe. Perhaps some of the eastern North American rhysodesmines combine with the other eastern tribes to form a monophyletic group. We can only speculate on this, but it becomes increasingly doubtful that all of the eastern rhysodesmine genera are contribal with *Rhysodesmus* and *Stenodesmus* in Mexico and Central America.

4. In conclusion, we again emphasize the importance of color, of which two basic patterns are displayed by the eastern xystodesmid fauna. In the Apheloriini and the Rhysodesmini (except for *Gyalostethus* and *Gonoessa,* which are comparatively dull; the color is unknown for *Parvulodesmus* and most species of *Caralinda)* the body is generally black and boldly marked by stripes or spots. In the Pachydesmini and Nannariini, body color is neither black nor boldly marked. Instead, it is brown to olive to reddish orange, with or without paler stripes. We have no phyletic interpretation; bold patterns may be mimetic and therefore convergent in the Rhysodesmini and Apheloriini, as appears to be true for certain species of the latter. However, the basic color patterns do apply at the tribal level, and coloration in xystodesmids is far more interesting and informative than is generally recognized. It should become a standard and integral part of future systematic studies in the family.

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